ANGIOSPERMS OF THE NORTHERN ROCKY MOUNTAINS: ALBIAN TO CAMPANIAN (CRETACEOUS) MEGAFOSSIL FLORAS[1]

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ABSTRACT

Synchronous first occurrences of pollen and leaves indicate that angiosperms entered the Northern Rocky Mountain (NRM) region during the Middle Albian, approximately 8 Ma later than such shifts in floras from southern Laurasia. The earliest angiosperm pollen and leaf flora corresponds to the Potomac sub-Zone IIB in that it exhibits a pretricolporate palynoflora and a comparable grade of evolution based on leaf rank. The Albian megaflora is characterized by abundant leaves of the Platanophyll, Protophyll, and Pentalobaphyll morphotypes. Sapindophylls are common and diverse. The flora contains early North American occurrences of the widespread Upper Cretaceous leaf form genera *Trochodendroides* and *Cinnamomoides*. Pentalobaphylls (Araliaephylls) appear early and assume a more important position in the lowland vegetation of the NRM region than in other regions. Magnoliidae, Hamamelididae, and Rosidae are represented in the Albian flora. The Albian megaflora is a regional variation of a largely cosmopolitan Laurasian flora. Latest Albian and Cenomanian megafloras suggest the development of north–south provincialism within the region. Post-Cenomanian to Campanian floras show gradual diversification with various Platanaceae and Hamamelidaceae as numerical dominants. Pinnate palms are present by the early Campanian. Higher-level taxa present in the region in the Early Campanian include Magnoliales, Laurales, Chloranthales, Nymphaeales, Menispermaceae, Trochodendrales, Platanaceae, Hamamelidaceae, Cercidiphyllales, Fagales, Rosidae, and palmate Dilleniidae.

In 1874 Leo Lesquereux stated:

The plants of the Dakota group, as known mostly by detached leaves, are stiking by their beauty, the elegance, the variety of their forms, and their size . . . it suffices to say that, at first sight, they forcibly recall those of the most admired species of our time . . . and the evident likeness of their facies . . . strikes the paleontologist and may lead him into error . . . for, really, when we enter into a more detailed analysis of these Cretaceous leaves, we are by and by forcibly impressed by the strangeness of the characters . . . which seem at variance with any of those recognized anywhere in the floras of our time . . . . Hence, this flora does not leave any satisfaction, any rest, to my mind.

In this paper I summarize and evaluate the evidence relevant to the paleoecology and evolution of early angiosperms in the Northern Rocky Mountain (NRM) region based on the megafloral record. The refinement of descriptive terminology for leaf architecture (Hickey, 1973, 1979; Dilcher, 1974) and elucidation of the phylogenetic significance of leaf morphology (Hickey & Wolfe, 1975), along with the U.S. National Cleared Leaf Collection and the U.S. Geological Survey Cleared Leaf Collection, have provided the framework for the present study.

The rich Cretaceous leaf fossil deposits of the western interior of North America have long been recognized for their importance to angiosperm paleobotany. Early treatments of these floras (during the late 1800s and early 1900s) mistakenly placed many leaf species into Recent genera. Even investigators who realized their predicament (see Lesquereux quote above) were ham-

pered in their attempts to interpret these leaves by the absence of appropriate operational paradigms. Throughout this report, genera of doubtful occurrence in the Cretaceous are marked with quotation marks. Where possible I have provided reappraisals of the affinities of these leaves in my discussions of Cretaceous leaf morphotypes and individual floras.

I cover the period of about 30 million years from the apparent advent of angiosperms during the Middle Albian to the middle of the Campanian. This includes the latter part of stage one of angiosperm evolution (Vakhrameyev, 1982), during which the group became established in restricted areas of a predominantly gymnosperm-dominated vegetation; and it includes most of stage two, in which angiosperms radiated explosively and displaced gymnosperms from many parts of the world.

The floras reported here come from British Columbia, Washington, Alberta, Montana, Wyoming, and Idaho (Figs. 1, 2).

Coniferous communities were the dominant form of vegetation in the world, at least through the Early Cretaceous (Hughes, 1969, 1976; Krassilov, 1981; Miller, 1977; Penny, 1969). Lower Cretaceous conifers from the NRM region are regarded as belonging to the Taxodiaceae, Araucariaceae, Podocarpaceae, Pinaceae, and Cheirolepidiaceae (Bell, 1956; Miller & LaPasha, 1984; Singh, 1964, 1971). With the exception of the Cheirolepidiaceae, which declined during the Albian, and the addition of the Cupressaceae which appear to have diversified during the middle and Late Cretaceous, these groups form the nucleus for the development in the Late Cretaceous of the North Pacific refugium (Vakhrameyev, 1982). Compressions and impressions of foliage and cones of Taxodiaceae, Cupressaceae, and Araucariaceae occur abundantly in coarser sediments throughout the region in the Upper Cretaceous (Berry, 1929a; Knowlton, 1905).

Ginkgophytes decrease in the region during the Albian, the latest flora in which they form an important component being the Lower Blairmore (Dawson, 1886; Bell, 1956), although foliage is reported from the Cenomanian Dunvegan Formation in northern Alberta (Bell, 1963), and *Salisburia* (cf. *Ginkgo*) seeds are reported as late as the Campanian Belly River flora (Dawson, 1886). The Ginkgophyte decline is delayed in the extreme northern latitudes. Although northslope Alaskan floras exhibit a notable decline in the Late Albian (Scott & Smiley, 1979), the group

remains important at least into the early Senonian in the Atane beds of Greenland (Seward & Conway, 1935), and into the Campanian in the Chignik Formation of central Alaska (Hollick & Martin, 1930). *Ginkgo* persists into the Paleogene in the Ft. Union Formation of Montana and the Willwood Formation of Wyoming (pers. obs.).

Fern communities of the Recent families Gleicheniaceae, Schizaeaceae, Dicksoniaceae, and Osmundaceae, and the extinct family Tempskyaceae occur abundantly in certain facies, a characteristic feature of the middle Cretaceous that Krassilov (1981) interpreted as evidence for extensive fern marshes. Pteridophytic communities colonized the widespread upper Albian and Cenomanian volcanic ash flats, occasionally being preserved in situ as in the Albino Member of the Mowry Shale in southwestern Montana (Crabtree, 1983; Vuke, 1982). Ferns such as *Gleichenia, Anemia, Sphenopteris, Cladophlebis, Tempskya, Coniopteris,* and *Onychiopsis* (but see Skog, 1985) are found throughout the region in the Albian and Cenomanian (Andrews, 1948; Andrews & Kern, 1947; Andrews & Pearsall, 1941; Ash & Read, 1976; Bell, 1956; Knowlton, 1917; Read & Brown, 1937; Seward, 1924). Post-Cenomanian floras show a decreasing representation of these genera, concomitant with increasing Polypodiaceae s.l. (pers. obs.).

Cycadophytes such as *Nilssonia, Zamites, Pseudoctenis, Ctenis,* and *Otozamites* decline rapidly after the Aptian. However, certain species persist in the Cenomanian Dunvegan flora (Bell, 1963) and the Turonian upper Frontier flora (Berry, 1929d), and *Zamites albertensis* Berry is abundant in the Campanian Allison flora of Alberta (Berry, 1929a). Cycadophytes also persist in the Late Cretaceous of Alaska (J. Wolfe, pers. comm.).

Sagenopteris, foliage of pteridosperms of the Caytoniales, is abundant during the Aptian and early Albian in the region (Bell, 1956; LaPasha & Miller, 1985) but is only rarely reported from the later Albian or from the Upper Cretaceous (see Winthrop flora in this report).

The relative abundance of major plant groups, and the entry of angiosperms into the region during the Middle and Upper Albian, can be seen in the histograms depicting the changing composition of the flora during the Middle and Upper Albian (Fig. 3). One histogram (Fig. 3A) is based on published megafossil floras and my own observations of unpublished floras. The other
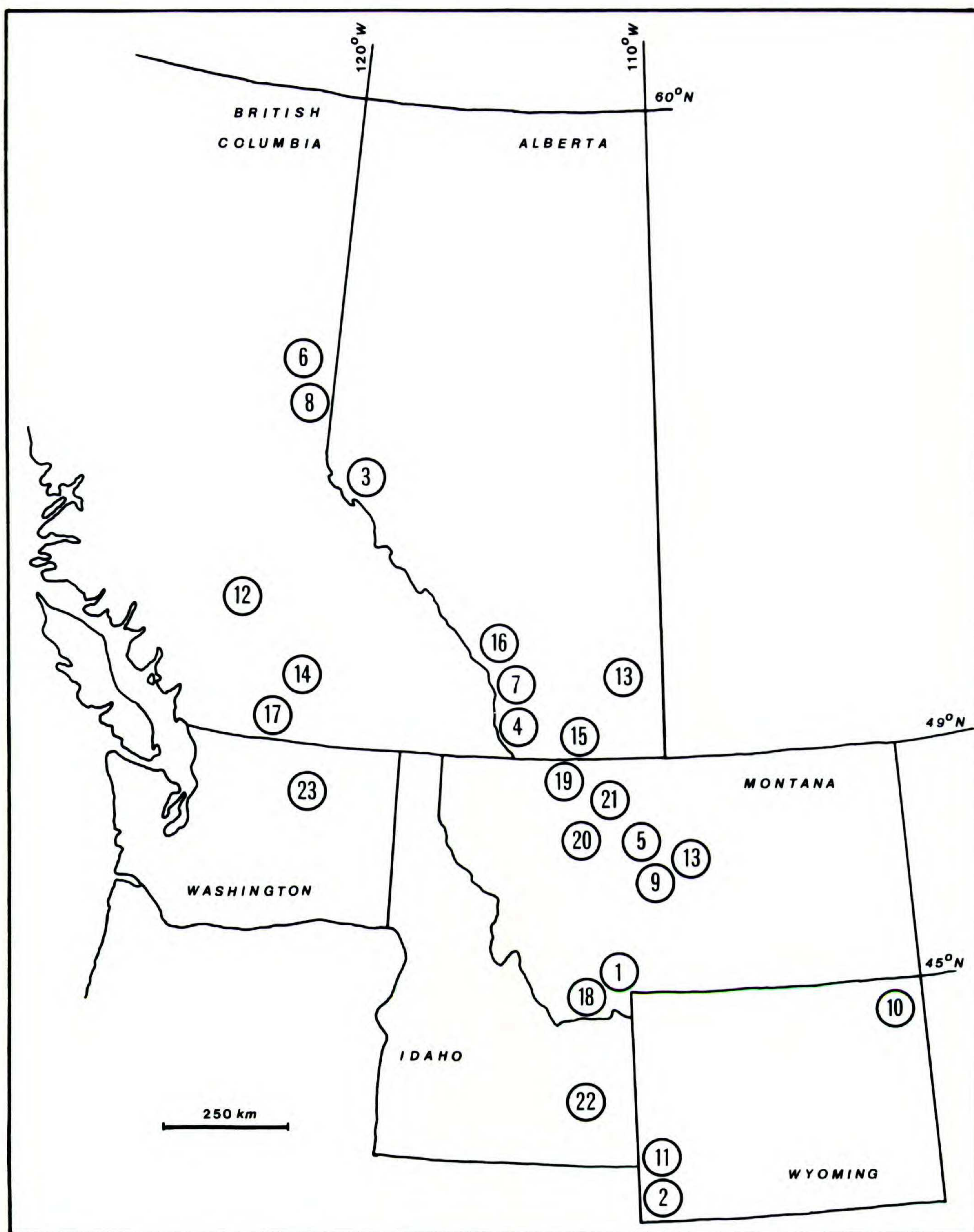
FIGURE 1. Geographic locations of plant megafossil collections in the northern Rocky Mountain region. Collection sites are numbered in alphabetical sequence. Names of sites appear in Figure 2. Appendix I contains additional information on locations.

(Fig. 3B) is based on published palynofloras. Percentages shown in the histograms were calculated by counting species of each major plant group within individual floras. These raw count totals were summed and a percentage calculated for each chronostratigraphic subdivision of the Albian. Megafossil floras show a bias towards preservation of vegetation adjacent to the deposi-

FIGURE 2.   Chronostratigraphic positions of plant megafossil collections in the northern Rocky Mountain region. Stage boundary dates according to Harland et al. (1982). Ages are in million years. Potomac Zones from Hickey & Doyle (1977). Stratigraphic placement of collections is based on my interpretation of the literature. Substage boundaries are based on my interpretation of western North American chronostratigraphy. Collections of uncertain age are indicated with question marks (see text and Appendix I for discussion).

tional environment; thus Figure 3A approximates the components of the lowland vegetation. Palynofloras used in Figure 3B were recovered mostly from marine and marginal marine environments, and thus more closely reflect the regional flora. From Figure 3A it is apparent that dramatic changes occurred in the lowland flora during the Middle and Upper Albian. In these environments angiosperms increased at the expense of ferns. Because this trend is not evident in Figure 3B, it is apparent that this early angiosperm radiation had its greatest impact on lowland vegetation.

PALEOGEOGRAPHIC AND GEOLOGIC SETTING

The northern Rocky Mountain region during most of the Cretaceous occupied a strip of land some several hundred kilometers wide, situated between the Pacific geosyncline/island arc to the west and the mid-continent epeiric sea to the east (McGookey et al., 1972; Williams & Stelck, 1975). Paleolatitudes may have varied up to ten degrees from the present range of 41°N in southern Wyoming to 60°N in northern Alberta and British Colombia. The paleocontinent positions of Smith et al. (1981) indicate that northern Alberta has

rotated 8–10° to the south since the Cretaceous, and southern parts of the region are presently approximately 2–5° farther south.

The first major expansion of the Cretaceous epeiric sea began in the Late Aptian and continued into the Albian, attaining its maximum extent in the late Middle Albian when it reached unbroken from the Arctic Ocean to the Gulf of Mexico (McGookey et al., 1972; Vuke, 1984; Williams & Stelck, 1975). The fluctuations of the sea initiated a famous series of transgressive–regressive clastic cycles of deposition that continued until the end of the Cretaceous (Waage, 1975). Geological formations in the region tend to parallel the north–south trending western shoreline of the seaway. Cretaceous sediments accumulated in terrestrial and marine environments to great thicknesses: up to 3,500 m in southwest Wyoming (Rubey et al., 1975) and 2,134 m in northwest Montana (Rice & Cobban, 1977). The source areas in present British Columbia, western Alberta, Idaho, Washington, Oregon, western Montana, and western Wyoming are inferred to have had considerable relief in order to account for the great thickness of accumulated sediments. Orogenic activity in the region was of long duration beginning in the Late Jurassic and Early Cretaceous with the uplift of the Nevadan Orogeny. The main thrusting of the Sevier Orogeny occurred throughout the Cretaceous, and the uplift of the Laramide Orogeny took place during and subsequent to the Campanian (Gilluly, 1963; Nichols et al., 1985).

PALEOCLIMATE

Generalized interpretations of paleoclimate, which include the North American Cretaceous, have been published by Frakes (1979), Habicht (1979), Lamb (1977), Schwarzbach (1974), and Vakhrameyev (1978). They recognized a general humidification in Laurasian climate from the Jurassic into the Cretaceous. This can be correlated with the widespread inundation of continental crust, a worldwide phenomenon in the Cretaceous, and the opening of the Atlantic Ocean.

Assessment of precipitation patterns and amounts during the Cretaceous in the NRM region is difficult with our present knowledge. Parrish et al. (1982) mapped the Cretaceous precipitation in the region as low to moderately low largely on account of the presumed orographic effect of the Rocky Mountains. However, they noted that the presence of important high latitude coals in the region, especially in the Late Cretaceous, may argue for heavy seasonal precipitation, perhaps a monsoonal effect.

Growth rings in fossil wood can be used to assess environmental influences on plant development (Creber, 1977; Creber & Chaloner, 1984, 1985; Fritts, 1976). Presence and degree of development of latewood and growth rings is generally correlated with available moisture. However, there are many examples of growth rings in trees living in regions of high rainfall. For instance, *Agathis* from Fiji, where annual rainfall is 2,000–6,000 mm, have well-developed growth rings (Ash, 1985). Nonetheless, I know of no exception to the formation of growth rings in the wood of trees growing in seasonal climates, and conversely, the absence of growth rings always indicates a nonseasonal climate (except perhaps in certain warm-climate swamp communities).

I examined 27 specimens of six species of coniferous woods from the Late Albian Vaughn Member of the Blackleaf Formation in northwest Montana in thin section for the presence and configuration of growth rings. Transverse sections could be grouped into three broad categories:

Category A. Woods exhibiting no growth rings.
Category B. Woods exhibiting broad (3–5 mm) and consistent growth rings with considerable latewood.
Category C. Woods exhibiting rings of variable width, including broad rings (up to 5 mm), pseudorings, and considerable latewood.

The Vaughn Member has been interpreted as a deltaic swamp deposit (Cannon, 1966) and was situated at about 55°N paleolatitude (Couillard & Irving, 1975). Cold-seasonality did not exist during the Albian at this paleolatitude. Seasonality as the result of low light during winter months may be a factor at 50°N, although I know of no literature on the subject. Broad-leaved evergreen forests are known to have extended to 65°N during the Cretaceous (Wolfe & Upchurch, 1986). Incomplete seasonal leaf-drop, formation of latewood, and cambial quiescence might well be associated with the northern extensions of this forest. Among several possible explanations for the mixed assemblage of woods, the following is suggested as the most plausible: the trees were growing in a warm, seasonally dry climate, with some species (Category A) living in areas of year-round groundwater. The pronounced develop-
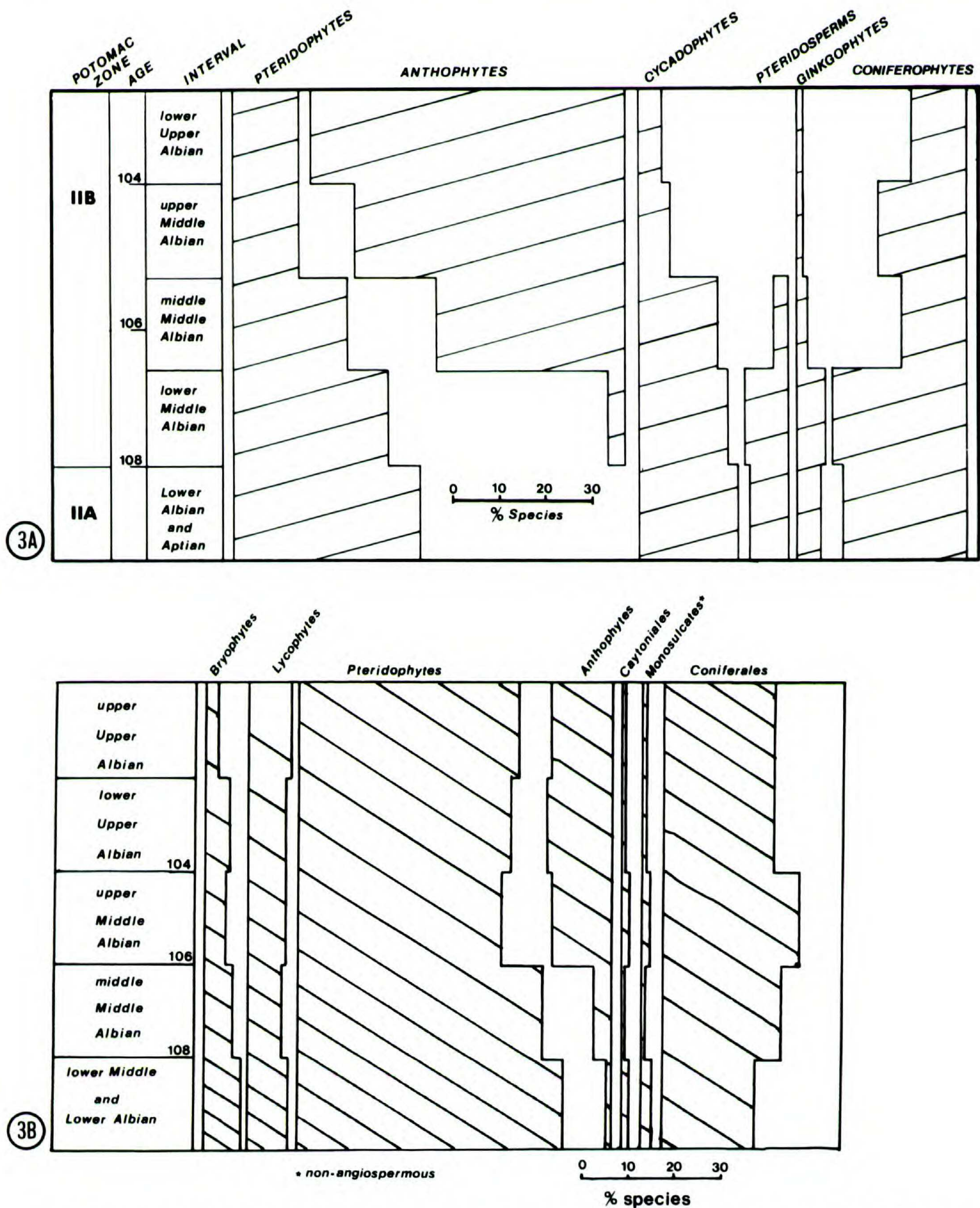
FIGURE 3. Relative abundance of major plant groups during the Albian of the northern Rocky Mountain region. Ages are in million years before present. **A.** Percentage occurrence of major plant groups based on megafossils. Occurrences of species for each plant group were tabulated for individual floras. These counts were then summed and a percentage calculated for each time interval as listed below. Total species counted for each interval are indicated in parentheses. Aptian and Lower Albian (119): Kootenai (Miller & LaPasha, 1984; LaPasha & Miller, 1985); Bullhead, Gething, and Luscar (Bell, 1956). Lower Middle Albian (150): Beaver Mines (Berry, 1929b; Bell, 1956; Mellon, 1967); Lower Gates Member (Stott, 1963). Middle Middle Albian (130): Upper Gates Member (Mellon et al., 1963); Pasayten (Penhallow, 1907; Bell, 1956); Kingsvale and Jackass Mountain (Bell, 1956); Fall River and Pre-Muddy (pers. obs.); Boulder Creek (Bell, 1956; Stott, 1963). Upper Middle Albian (150): Mill Creek (Dawson, 1886; Berry, 1929c; Bell, 1956; Mellon, 1967). Lower Upper Albian (89): Crowsnest (Bell, 1956; Mellon, 1967); Summit, Sun River, and Black Eagle (pers. obs.). **B.** Percentage occurrence of major plant groups based on microfossils. Percentages calculated as above. Assignment of spores

ment of latewood in Categories B and C suggests seasonality in precipitation. An alternative explanation is that low light availability in winter induced latewood formation in some species but not others.

Late Albian or Cenomanian woods of *Cupressinoxylon* sp. (Andrews & Kern, 1947) and *Paraphyllanthroxylon idahoense* Spackman (1948) from the Wayan Formation in southeastern Idaho have no prominent growth rings and can be seen as evidence for equable year-round temperatures. These woods suggest either the absence of seasonality in precipitation or that the trees grew in swampy or other well-watered habitats.

Later in the Cretaceous there is further evidence for seasonal or low precipitation in the region, possibly related to the mountain building of the Laramide Orogeny. The Campanian Two Medicine Formation in northwestern Montana includes caliches, desiccated carbonate nodules, and sandstone bodies of episodic rivers that indicate a seasonal wet–dry climate, with the dry season longer (Lorenz, 1981). The abundance of large (mesophyll and megaphyll size), apparently deciduous leaves in the Two Medicine flora supports such a climatic seasonality, although the leaves can be interpreted alternatively as indicative of successional communities. Low or seasonal precipitation is further indicated by a substantial notophyllous evergreen component of coriaceous leaves typically without drip tips. Coniferous woods from the lower Two Medicine exhibit pronounced growth rings of highly variable thickness (Crabtree, pers. obs).

Oxygen isotope ratios are used most accurately to estimate maximum paleotemperature and to establish temperature trends of ocean waters (Frakes, 1979). Oceanic temperatures can be used to estimate temperatures on nearby land masses. Since the NRM region during much of the Cretaceous was a relatively narrow land mass positioned between the Pacific Ocean on the west and the epeiric seaway on the east, it is likely that oceanic temperatures are significant for approximation of the land temperatures.

Isotopic ratios from the continental platform off the Soviet Union (Douglas & Savin, 1975) indicate a Cretaceous temperature maximum in the Albian, followed by cooling in the Late Albian and Cenomanian. Subsequently, a rewarming occurred in the early Senonian before a Maastrichtian cooling (but see also Boersma, 1984). The Albian maximum is probably the warmest period that the world has experienced since Paleozoic time (Frakes, 1979). Latitudinal gradients in surface water temperatures were less steep during the Cretaceous, and the average temperatures of deep water appear to have been significantly higher than at present (Schopf, 1980). Mid and Late Jurassic oxygen isotope ratios from Montana and Wyoming indicate that the surface water had a maximum of 20°C (Donn & Shaw, 1977). Polar ice was unknown during the Cretaceous, and Frakes (1979) hypothesized that north polar surface water was no cooler than 7–19°C and may have been at the high end of this range based on isotopic paleotemperatures of about 15°C for putative North Pacific Deep Water from the equatorial Pacific (Stevens, 1971). A computerized model of surface water temperatures for an ice-free Arctic predicts a temperature increase of 7–10°C over the present 0–5°C temperature range (Sellers, 1969).

Hermatypic coral reefs occur in tropical and subtropical oceans. Because modern reefs form only when minimum water temperatures exceed 18°C, their fossil distribution can be used to estimate minimum oceanic paleotemperatures. The Mesozoic distributions of reefs (Newell, 1971; Beauvais, 1973) indicate that oceanic currents in temperate latitudes were significantly warmer than at present. A reef from the Jurassic of Wyoming (Beauvais, 1973) indicates that they formed as far north as 50°N paleolatitude, but there is doubt that the Wyoming reef is hermatypic (G. Stanley, pers. comm.). Nonetheless, bona fide hermatypic reefs are present during the Jurassic and Cretaceous at latitudes 10–20° north of their present distribution.

Several papers discuss paleofloristic climatic zonation during the Cretaceous based on the composition of eastern Asian megafloras (Krassilov, 1973a, 1975, 1978) and microfloras

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← and pollen to major plant groups follows the interpretations of Singh (1971) and Norris (1967). Numbers in parentheses after age below indicate total number of species counted for that interval. Lower Albian and lower Middle Albian (179): McMurray-Clearwater (Vagvolgyi & Hills, 1969); Loon River (Singh, 1971). Middle Middle Albian (206): Harmon (Singh, 1971); Upper Grand Rapids (Norris, 1967). Upper Middle Albian (200): Cadotte (Singh, 1971); Joli Fou (Norris, 1967). Lower Upper Albian (184): Paddy (Singh, 1971); Viking (Norris, 1967). Upper Upper Albian (213): Shaftsbury (Singh, 1971); Upper shale (Norris, 1967).
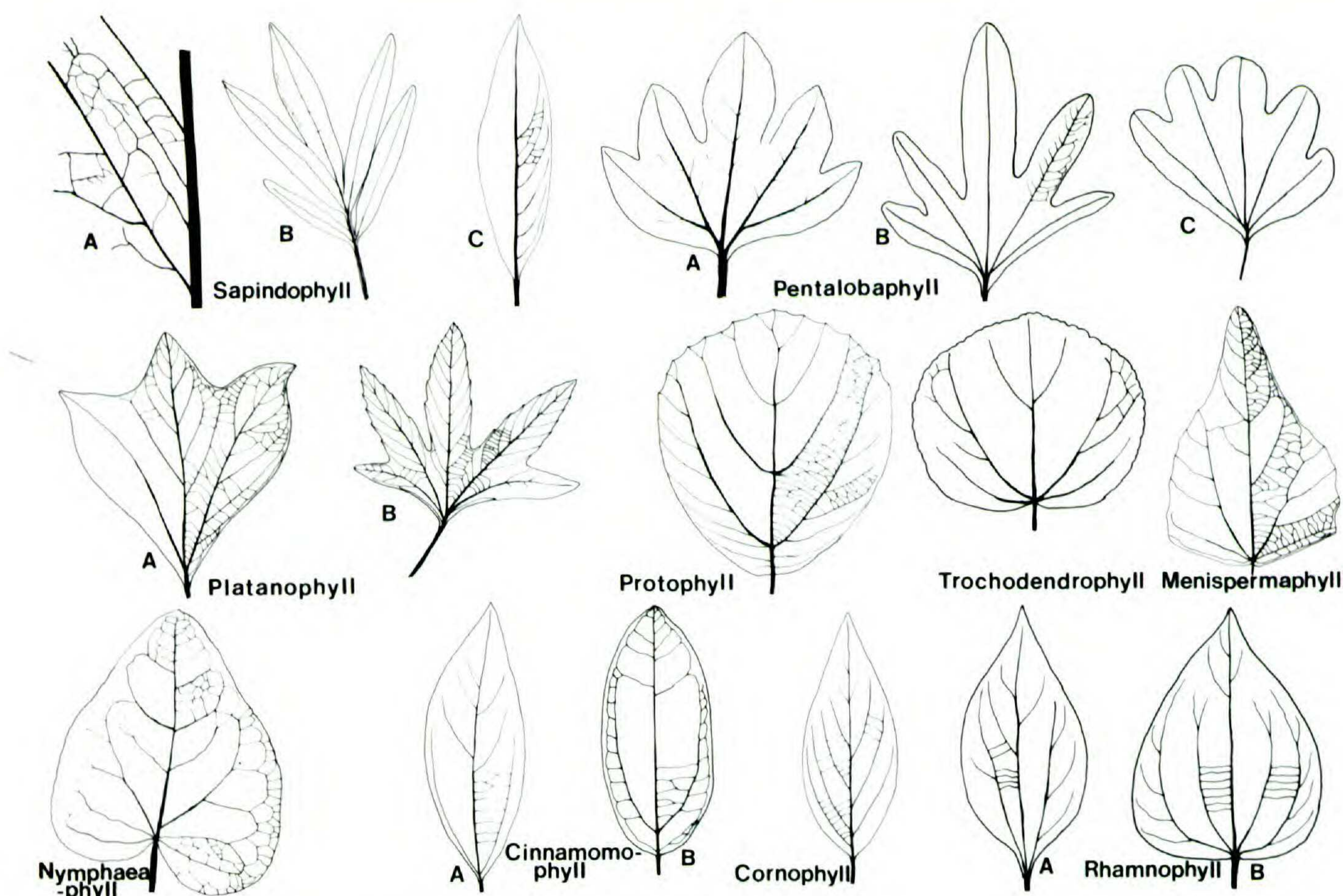
FIGURE 4. Cretaceous dicotyledonous leaf morphotypes. Sources of previously published drawings are indicated. SAPINDOPHYLL: —A. cf. *"Ficus" beckwithii* Lesquereux (Crabtree), Dakota Formation, Golden, Colorado (Peabody Museum Paleobotanical Collection no. 5849). —B. *Sapindopsis magnifolia* Fontaine, Patapsco Formation, Virginia (fig. 17 in Doyle & Hickey, 1976). —C. Generalized leaflet. PENTALOBAPHYLL: —A. *Araliaephyllum obtusilobum* Fontaine, Patapsco Formation, Virginia (pl. 164, fig. 3 in Fontaine, 1889). —B. *Araliaephyllum westonii* (Dawson) Bell. —C. *Araliaephyllum rotundata* Dawson. PLATANOPHYLL: —A. *Araliopsoides breviloba* Berry, Raritan Formation, Maryland (pl. 86, fig. 2 in Berry, 1916). —B. *"Aralia" saportanea* Lesquereux, Dakota Formation, Kansas (pl. 9, fig. 2 in Lesquereux, 1883). PROTOPHYLL: Generalized leaf. TROCHODENDROPHYLL: Generalized leaf. MENISPERMAPHYLL: *Menispermites obtusilobus* Lesquereux, Dakota Formation, Kansas (pl. 15, fig. 4 in Lesquereux, 1883). NYMPHAEAPHYLL: *"Cocculus" haydenianus* Ward, Fort Union Formation, Montana (pl. 59, fig. 2 in Ward, 1885). CINNAMOMOPHYLL: —A. *"Cinnamomum" sezannense* Watelet, Dakota Formation, Kansas (pl. 12, figs. 6, 7 in Lesquereux, 1892). —B. Generalized leaf. CORNOPHYLL: *"Cornus" forchhammeri* Heer, Raritan Formation, Maryland (pl. 82, fig. 1 in Berry, 1916). RHAMNOPHYLL: —A. *"Cinnamomum" intermedium* Newberry (pl. 29, fig. 7 in Hollick, 1906). —B. Generalized leaf.

(Chlonova, 1980). Krassilov's papers propose four intuitively based, latitudinal climatic zones: boreal, temperate, warm-temperate, and subtropical. Relative to these zones, the NRM region is closest to the warm-temperate zone based primarily on the presence in the Albian and Cenomanian of several thermophilous ferns and temperate *Nilssonia,* and in the Campanian by the presence of palms and large-leaved deciduous dicots. A position in the warm-temperate zone is consistent with Campanian floras in Sakhalin, Amur, Altai, western Greenland, and Vancouver Island (Krassilov, 1981). Vakhrameyev (1978) placed the NRM region straddling the boundary between his temperate-warm and subtropical humid zones for the Early Cretaceous. This placement is based on the presence of *Tempskya* and *Cycadeoidea* in Montana and South Dakota. The boundary shifts approximately 100 km to the north in his Late Cretaceous reconstruction, placing it just north of the present 49th parallel (about 55°N paleolatitude). The Late Cretaceous temperate-warm humid zone is based on the occurrence of *Nilssonia* and *Pseudoprotophyllum,* and the subtropical humid zone is based on palms and *Dewalquea.*

Smiley (1967), basing his arguments primarily on North American high-latitude floras, indicated that the climate gradually warmed from the Jurassic into the Albian, after which a general cooling occurred through the Late Cretaceous (at the same time as Alaska was rotating to the south).

Scott & Smiley (1979) reported on the micro- and megafossil flora from the north slope of Alaska. Their treatment indicates that northern floras remain predominantly gymnospermous-pteridophytic until the end of the Late Albian, that they do not exhibit *Classopollis* pollen in any significant quantity (but see Herngreen & Chlonova, 1981), and that they are allied to more southerly Albian floras by abundant spores of Gleicheniaceae and Schizaeaceae. Vakhrameyev (1982) recognized the Early Cretaceous as a time of increasing aridity followed by "humidification and some cooling" by the Albian. Cooling was not extreme, however, as the presence of frost-sensitive ferns throughout the Lower Cretaceous at high latitudes indicates, and did not continue, since palms in the Senonian indicate a generally equable year-round temperature. Krassilov (1973a, 1975, 1981) stated that Late Cretaceous climates in Asia warm into the Campanian and subsequently cool through the end of the Cretaceous.

THE EARLY ANGIOSPERM FLORA

Hickey & Wolfe's (1975) synthesis of the systematic implications of leaf morphology among extant dicots enables paleobotanists to assess the relationship of fossil taxa by extrapolation. Krassilov (1977) and Hickey (1984) used a series of informal descriptive names for early angiosperm leaf fossils that attempt to unify fossil species with similar morphology. Such leaf morphotypes are especially appropriate for Early Cretaceous dicot leaves that have been placed mistakenly in extant genera. Morphotypes are best viewed as serving as a descriptive terminology in lieu of revision.

Most important morphotypes from western North American mid-Cretaceous floras are illustrated in Figure 4 (see also Hickey, 1984). The drawings are based in some cases on individual taxa and in others on an idealized composite of several different taxa (see figure legend). In all cases the drawings represent the general form or range of forms present in the morphotype. Table 1 lists the morphotypes along with the genera that have been used in the past for species belonging to each. Extant genera, such as *Populus*, which has been mistakenly regarded as embracing a large number of disparate fossil taxa, may be listed under more than one morphotype. Extant genera cannot be demonstrated from the mid Cretaceous, with rare exceptions (Doyle,

1969; Walker & Walker, 1984). Extinct genera for which the type species is of Cretaceous age are included under the appropriate morphotype according to the type description. Fossil genera for which the type is younger than Late Cretaceous have not been considered for inclusion, reflecting the intended focus on early angiosperms. Thus, *Laurophyllum* Saporta is named from Tertiary material; hence, I consider it inappropriate as a generic placement for Early Cretaceous angiosperms. Morphotypes, since they are not formal taxonomic classifications, have no types.

I have chosen to discuss the early angiosperm flora of the NRM region using the leaf morphotypes as a descriptive base. For each morphotype I provide a brief description using the leaf architectural terminology of Hickey (1979). In addition, I provide particulars relevant to the distribution in time and space for each morphotype along with observations on relative abundance and diversity. Possible relationships for each morphotype are discussed individually and summarized in Table 1.

The occurrence and distribution of early angiosperms in the NRM region is presented in Table 2, which encompasses the first five million years of angiosperm history in the region. Where possible, species are grouped according to morphotype. All Albian and major floras from the region are included, in addition to several previously unreported collections. Names of taxa appear as originally published except for floras examined by myself, for which I have provided identifications. Ages and locations of floras appear in Figures 1 and 2 and in Appendix I.

Pentalobaphyll (Araliaephyll). Leaves simple, orbicular, 3–5-lobed. Margin entire. Base ± cuneate. Primary venation palinactinodromous, with 3 primary veins diverging from above top of petiole, and 2 subprimary veins branching from lateral primaries just above base. Secondary venation eucamptodromous, rather weakly developed. Tertiary venation reticulate to transverse, AR to AO. Higher order venation and cuticle not observed.

This very distinctive group is first recognized in the region during the Middle Albian. Pentalobaphylls are lobate leaves with five principal veins, the two outermost of which originate as suprabasal branches from the lateral primary veins (Fig. 4). *Araliaephyllum obtusilobum* Fontaine is included in this group on the basis of the

TABLE 1. Botanical affinity and important genera for Cretaceous leaf morphotypes.

Morphotypes	Important genera[1,2]	Botanical affinity
Sapindophyll	*Fontainea* Newberry, *Sapindopsis* Fontaine, *"Andromeda," "Diospyros," "Ficus," "Laurus," "Rhus," "Salix," "Sapindus," "Staphylea"*	Rosidae
Pentalobaphyll	*Araliaephyllum* Fontaine, *Sterculites* Dawson, *"Aralia," "Hedera," "Liquidambar," "Sassafras," "Sterculia"*	Unknown; possibly Rosidae or Magnoliidae (Laurales)
Platanophyll	*"Araliopsis," Araliopsoides* Berry, *Aspidophyllum* Lesquereux, *Platanophyllum* Fontaine, *Pseudoaspidophyllum* Hollick, *"Aralia," "Platanus," "Sassafras"*	Hamamelididae–Platanales
Protophyll	*Cissites* Debey, *Credneria* Zenker, *Paracredneria* Richter, *Protophyllum* Lesquereux, *Pseudoprotophyllum* Hollick, *Viburnites* Lesquereux, *"Alnus," "Betula," "Cissus," "Parrotia," "Platanus," "Populus," "Tilia"*	Polyphyletic within Hamamelididae—probably Platanales and Hamamelidales
Trochodendrophyll	*Trochodendroides* Berry, *"Cercidiphyllum," "Cocculus," "Grewia," "Paliurus," "Populus," "Smilax," "Zizyphus"*	Trochodendrales and Crecidiphyllales
Menispermaphyll	*Menispermites* Lesquereux, *"Ampelopsis," "Cissampelopsis," "Cocculus," "Hedera"*	Unknown; possibly Ranunculiidae
Nymphaeaphyll	*Castaliites* Hollick, *Hederaephyllum* Fontaine, *Nelumbites* Berry, *Paleonuphar* Hollick, *Populophyllum* Fontaine, *Proteaephyllum* Fontaine, *"Castalia," "Hedera"*	Magnoliid–Nymphaeales
Magnoliaephyll	*Liriodendropsis* Newberry, *Liriophyllum* Lesquereux, *Magnoliaephyllum* (Krasser) Seward, *"Bauhinia," "Ficus," "Laurus," "Liriodendron," "Magnolia," "Persea," "Sassafras"*	Polyphyletic; some Magnoliidae, possibly Laurales, Magnoliales.
Cinnamomophyll	*Cinnamomoides* Seward, *"Benzoin," "Cinnamomum," "Cocculus," "Litsea," "Oreodaphne," "Paliurus," "Zizyphus"*	Polyphyletic; some probably Laurales
Cornophyll	*Cornophyllum* Newberry, *"Andromeda," "Cornus," "Diospyros," "Ficus" "Rhamnus"*	Polyphyletic; some possibly Rosidae
Rhamnophyll	*Macclintockia* Heer, *"Cinnamomum," "Ficus," "Paliurus," "Piper," "Rhamnus," "Smilax," "Zizyphus"*	Polyphyletic; some possibly palmate Dilleniidae

[1] See text for criteria used for inclusion of genera.
[2] Quotation marks indicate extant genera mistakenly identified in the Cretaceous flora.

characteristic venation, although this and several other species may have three-lobed leaves. Doyle & Hickey (1976) include this species in their Platanoid line, based primarily on the palinactinodromous primary venation. The palmate lobing and palinactinodromous venation of the Pentalobaphylls is here considered to be insufficient evidence to establish relationship with the Platanoid line when viewed along with the balance of leaf-morphological characters. Pentalobaphylls show leaf-morphological characters, including entire margins, eucamptodromous secondary venation, and weak tertiary venation, which serve to distinguish the group from Platanophylls. The tendency towards orthogonal branching of tertiary and quaternary veins so characteristic of Platanophylls is absent in Pentalobaphylls.

Certain palmate leaves from the Albian flora cannot be accommodated under either the Pentalobaphyll or Platanophyll morphotype. These include *"Liquidambar" fontanella* Brown, with glandular-toothed margins, and *"Sassafras" bradleyi* Brown, which has smooth margins but lacks the suprabasal lateral branches characteristic of Pentalobaphylls.

Fritel (1914) recognized seven species of Pentalobaphylls that were widespread throughout the Laurasian landmass during the Late Albian and Cenomanian. He characterized the group based

primarily on the three basal primary veins, the lateral two of which give off prominent lateral veins just above the point of radius, and on the camptodromous secondary venation. However, he included forms exhibiting serrate margins, craspedodromy, and orthogonal reticulate higher order venation such as "*Aralia*" *saportanea* Lesquereux, which I assign to the Platanophylls.

Pentalobaphylls are perhaps the most abundant dicots from Albian floras of the NRM region. Albian Pentalobaphylls from Wyoming (Fig. 5), Montana (Fig. 6), and Alberta (Figs. 7–9) are representative of the group. Fritel (1914) placed the Alberta species *Araliaephyllum westonii* (Dawson) Bell and "*Aralia*" *rotundata* Dawson into synonymy with *Araliaephyllum kowalewskiana* (Saporta & Marion) Fritel from Europe. A more thorough treatment of the group is needed before such conclusions are substantiated. Cuticular detail for the group is unknown with the exception of the Senonian *Araliaephyllum polevoi* (Krystofovich) Krassilov (1973b) from the eastern Soviet Union, for which a similarity to *Sassafras* and *Lindera* is suggested. G. Upchurch (pers. comm.) has suggested a lauralean affinity for leaves of the *A. polevoi* group based on cuticular detail, sinus bracing, mesophyll secretory glands, and possible basilaminar secondary veins. The secondary and tertiary venation (Figs. 4, 8) in this group suggests rosid affinity.

Platanophyll. Leaves simple. Margins entire or serrate, lobed or unlobed. Primary veins usually 3, palinactinodromous with several pectinal secondaries on laterals. Secondary veins straight, forking or exmedially branched, craspedodromous to teeth, brochidodromous if margin entire. Tertiaries and quaternaries forming an orthogonal network. Teeth platanoid, glandular processes often nipple-shaped. Cuticular structure in Upchurch (1984b), Krassilov (1973b), Kvaček (1983), Bůžek et al. (1967), Němejc & Kvaček (1975).

Members of this widespread Laurasian morphotype date from the Middle Albian in North America. The earliest occurrence from the NRM region is "*Platanus*" sp. (Fig. 10) from the upper Middle Albian of Alberta (Bell, 1956). Platanophylls of Middle and Late Albian age occur in several floras from the NRM region (Table 2). A particularly rich assemblage of Platanophylls occurs in the Late Albian Blackleaf Formation in Montana (Figs. 11–14). Several poorly preserved specimens representing the group are reported

from the Middle and Upper Albian of Alberta (Bell, 1956). As in the Albian flora of Alaska (Hollick & Martin, 1930) and eastern North America (Doyle & Hickey, 1976), the group is most frequently encountered in coarse fluvial sediments.

Araliopsoides cretacea (Lesquereux) Berry is an early member of this complex and is reported from the Late Albian in the Patapsco Formation in eastern North America (Hickey & Doyle, 1977). *Araliopsoides cretacea* is also reported from the Cenomanian of Texas (Berry, 1922b), Kansas (Lesquereux, 1874), and eastern North America (Berry, 1916; Hickey & Doyle, 1977). In the NRM region *A.* cf. *cretacea* is known from the Late Albian Summit locality in the Blackleaf Formation (Table 2, Fig. 14).

Platanophylls are typically more abundant in higher latitude floras (above approximately paleolatitude 45°N), and the group may appear in the NRM region before eastern North America. Little debate exists over the platanoid affinities of Platanophylls, but the precise timing of the origin of the Recent order and family remains unresolved. Recent *Platanus* is reported as being of Senonian age on the basis of pollen morphology (Pactlova, 1978), with pollen of platanaceous character recorded from the Albian (Pactlova, 1982). Němejc & Kvaček (1975) proposed on the basis of cuticular analysis that Cenomanian *Credneria* spp. (here considered Protophylls) from Bohemia are related to the platanaceous line. Early Platanophylls are related to, and convergent with, other groups of the emerging Hamamelididae, especially the Protophylls.

Fructifications regarded as of platanoid affinity are widespread in the Late Albian and Cenomanian of North America. Notable among these are records of "*Sparganium*" from Washington (Fig. 35) and Wyoming (Fig. 41; Brown, 1933a), and "*Platanus*" from Greenland (Seward & Conway, 1935) and Kansas (Lesquereux, 1892). For further discussion of Cretaceous fructifications of platanoid affinity see Dilcher (1979) and Crane et al. (1986).

Platanophylls are allied to Protophylls on the basis of well-defined, orthogonal-reticulate, tertiary and quaternary venation. Palinactinodromous venation and a greater tendency towards lobation distinguishes the Platanophylls from the Protophylls, which have pinnate organization (Fig. 4). I have chosen to segregate these leaves in the hope that the Cenomanian *Cissites-Betulites-Alnites* complex (Protophylls) might be

TABLE 2. Early angiosperm flora from the northern Rocky Mountain region.[1,2,3]

	Beaver Mines (4) A	B	C	Lower Gates (6a)	Upper Gates (6b)	Fall River (10)	Pre-Muddy (18)	Boulder Creek (6c) A	B	Pasay-ten (17) A	B	Kingsvale (14)	Jackass (12)	Mill Creek (16) A	B	C	D	Summit (19)	Sun River (20)	Black Eagle (5)	Crows-nest (7) A	B
Sapindophyll																						
Celastrophyllum acutidens Fontaine										X	X				X	X						
Celastrophyllum sp.																X						
cf. *Celastrophyllum* sp.																				X		
Daphnophyllum dakotense Lesquereux													X									
Fontainea grandifolia Newberry							X								X	X					X	
Fontainea cf. *F. grandifolia* Newberry				X																		
Fontainea sp.																X						
"Laurus" crassinervis Dawson													X									
"Myrica" serrata Penhallow								X														
Proteoides daphnogenoides Heer													X									
"Quercus" flexuosa? Newberry								X														
"Salix" inaequalix? Newberry												X				X						
cf. *"Rhus" powelliana* Lesquereux							X															
Sapindopsis angusta (Heer) Seward & Conway	X									X	X					X					X	
Sapindopsis cf. *angusta*																						X
Sapindopsis sp. aff. *angusta*		X																				
Sapindopsis belviderensis Berry					X										X	X						
Sapindopsis brevifolia? Fontaine	X																					
Sapindopsis cf. *brevifolia*																						X
Sapindopsis magnifolia Fontaine																X						
Sapindopsis cf. *magnifolia*					X																	X
Sapindopsis sp.					X																	
Sapindopsis sp.						X																
cf. *Sapindopsis* sp.																	X					
cf. *Sapindopsis* sp.																		X				
Pentalobaphyll																						
"Aralia" rotundata Dawson													X									
"Aralia" westonii Dawson													X									

TABLE 2. Continued.

	Beaver Mines (4)			Lower Gates (6a)	Upper Gates (6b)	Fall River (10)	Pre-Muddy (18)	Boulder Creek (6c)		Pasayten (17)		Kingsvale (14)	Jackass (12)	Mill Creek (16)				Summit (19)	Sun River (20)	Black Eagle (5)	Crowsnest (7)	
	A	B	C					A	B	A	B			A	B	C	D				A	B
Araliaephyllum westonii (Dawson) Bell												X		X	X	X				X		X
Araliaephyllum? sp.				X																		
Araliaephyllum sp.																		X				
"*Liquidambar*" *integrifolium* Lesquereux												X										
"*Sassafras*" *mudgii?* Lesquereux													X									
cf. "*Sterculia*" *mucronata* Lesquereux						X																
"*Sterculia*" *vetustula* Dawson												X										
"*Sterculia*" sp.																						X
Protophyll																						
Alnites insignis? Dawson												X										
Cissites? sp.				X																		
cf. *Cissites* sp.								X														
"*Platanus*" *affinis* Lesquereux												X										
"*Platanus*" *affinis* var. *ampla* Dawson												X										
Populites dawsonii Bell														X	X							X
Populites cf. *dawsonii*				X																		
Populites sp.																			X			
cf. *Protophyllum* sp.																		X				
Platanophyll																						
"*Aralia*" *wellingtoniana* Lesquereux				X																		
cf. "*Aralia*" *wellingtoniana*																		X				
Araliopsoides cf. *cretacea* (Newberry) Berry																		X				
cf. *Aspidophyllum trilobatum* Lesquereux																			X			
Platanophyllum sp.																			X			
Platanophyllum sp.				X																		
"*Platanus*" *heeri* Lesquereux												X										
"*Platanus*" sp.								X														
"*Platanus*" sp.										X				X								
"*Platanus*" sp.																			X			X
"*Platanus*" n. sp.																			X			
"*Sassafras*" *cretaceum* Newberry							X															
Trochodendrophyll																						
"*Cercidiphyllum*" sp.							X															

TABLE 2. Continued.

	Beaver Mines (4) A	B	C	Lower Gates (6a)	Upper Gates (6b)	Fall River (10)	Pre-Muddy (18)	Boulder Creek (6c) A	B	Pasayten (17) A	B	Kingsvale (14)	Jackass (12)	Mill Creek (16) A	B	C	D	Summit (19)	Sun River (20)	Black Eagle (5)	Crowsnest (7) A	B
Menispermites potomacensis Berry								X				X										
Trochodendroides ("*Cercidiphyllum*") *potomacensis* (Ward) Bell												X			X	X						X
Nymphaeaphyll																						
"*Hedera*" *ovalis*? Lesquereux												X										
Menispermites reniformis Dawson								X	X	X				X	X							
Menispermites sp.															X							
Nelumbites sp.												X										
Nymphaeites sp.																			X			
Magnoliaephyll																						
"*Magnolia*" *alternans* Heer												X										
"*Magnolia*" *magnifica* Dawson												X				X						
Cornophyll																						
"*Ficus*" *fontainii*? Berry								X														
Laurophyllum debile Dawson												X										
Rhamnites sp.													X									
"*Rhamnus*" sp.											X											
Cinnamomophyll																						
"*Cinnamomum*" *canadense* Dawson												X										
Cinnamomoides ovalis (Dawson) Bell												X			X	X					X	X
Cinnamomoides cf. *ovalis* (Dawson) Bell																						X
Cinnamomoides sp.																					X	
Cinnamomoides sp.																						X
Cinnamomoides sp.																			X			
Macclintockia cretacea Heer												X										
"*Paliurus*" *ovalis* Dawson												X	X									
Uncertain																						
Capparites? sp.												X										
Dicotylophyllum sp.																X						
"*Ficus*" cf. *fontainii*																X						
"*Ficus*" *ovatifolia* Berry				X										X	X							
cf. "*Ficus*" *ovatifolia* Berry																			X			

TABLE 2. Continued.

	Beaver Mines (4) A	B	C	Lower Gates (6a)	Upper Gates (6b)	Fall River (10)	Pre-Muddy (18)	Boulder Creek (6c) A	B	Pasayten (17) A	B	Kingsvale (14)	Jackass (12)	Mill Creek (16) A	B	C	D	Summit (19)	Sun River (20)	Black Eagle (5)	Crowsnest (7) A	B
Juglandites cretacea Dawson														X								
"*Magnolia*"? sp.															X							
"*Magnolia*" sp.								X														
"*Magnolia*" sp.																X						
"*Magnolia*" n. sp.																X						
"*Magnolia*"? sp.																X						
Menispermites? sp.																X						
Myrtophyllum boreale Seward & Conway												X										
"*Populus*" cf. *berggrenii* Heer														X								
"*Populus*" *cyclophylla* Heer									X													
Quercophyllum? sp.																X						
"*Quercus*" *coriacea* Newberry									X													
"*Salix*"? sp.																X						
"*Salix*" sp.									X													
"*Sassafras*" *parvifolium* Fontaine					X																	

[1] Numbers in parentheses refer to geographic and stratigraphic position of floras as indicated in Figures 1 and 2.

[2] All species are included as originally cited in the references given below. I have identified the species from the Summit, Sun River, Black Eagle, Fall River, and Pre-Muddy collections.

[3] Vertical rows indicate single floristic references as follows: (4)A—Berry, 1929b. (4)B—Bell, 1956. (4)C—Mellon, 1967. (6a)—Stott, 1963. (6b)—Mellon et al., 1963. (6c)A—Bell, 1956. (6c)B—Stott, 1963. (17)A—Penhallow, 1907. (17)B—Bell, 1956. (14)—Bell, 1956. (12)—Bell, 1956. (16)A—Dawson, 1886. (16)B—Berry, 1929c. (16)C—Bell, 1956. (16)D—Mellon, 1967. (7)A—Bell, 1956. (7)B—Mellon, 1967. (10), (18), (19), (20), and (5)—Crabtree, this report. It should be noted that W. A. Bell, in his capacity as paleobotanist with the Geological Survey of Canada, provided the identifications for megafossils reported in Stott (1963), Mellon (1967), and Mellon et al. (1963).

better understood. I suggest that Protophylls are more similar to mainline Hamamelidales on the basis of leaf architecture than are Platanophylls, which are closer to the platanoid line of Hamamelids.

Protophyll. Leaves simple. Margin entire to dentate, occasionally lobed. Venation pinnate, the basal secondaries sometimes strengthened considerably and bearing pectinals. Secondary and higher order venation similar to Platanophylls. Cuticular details in Němejc & Kvaček (1975) and Krassilov (1973b).

Richter (1905) monographed *Credneria* Zenker and *Paracredneria* Richter.

Protophylls can usually be distinguished from Platanophylls by the basically pinnate venation and by the more consistent craspedodromy of the secondary veins (Fig. 4). However, in many cases the two morphotypes intergrade to the extent that recognition is difficult. Protophylls are common in the NRM region but do not exhibit the diversity or dominance found in the coarse facies of the Cenomanian Dakota flora of Nebraska and Kansas (Lesquereux, 1892). Several species from the Albian floras of Alberta are placed in this morphotype (Table 2). Protophylls are present in the Blackleaf flora (Fig. 15). Basal venation in Platanophylls and Protophylls is compared in Figures 16 and 17.

Sapindophyll. Leaves even to odd pinnatifid or pinnately compound. Leaflets opposite or alternate, sometimes decurrent on rachis. Margins entire to serrate. Teeth apparently cunonioid. Petiole stout. Petiolule stout. Primary vein stout. Secondary veins eucamptodromous or semicraspedodromous, arched-ascending, often numerous, diverging at ± uniform angle of 35–50°. Intersecondary veins typically present. Tertiaries weakly percurrent, transverse, AR but highly variable. Quaternaries irregularly reticulate. Cuticle and tooth morphology in Upchurch (1984b).

This unique Lower and mid-Cretaceous morphotype encompasses fossils with pinnatifid or pinnately compound leaves (Fig. 4). Rachises with attached leaflets have been reported as *Sapindopsis* Fontaine and *Fontainea* Newberry. The widespread Laurasian species "*Andromeda*" *parlatorii* Heer, "*Ficus*" *daphnogenoides* (Heer) Berry, "*F.*" *beckwithii* Lesquereux, "*Sapindus*" *morrisonii* Lesquereux, and "*Rhus*" *powelliana* Lesquereux represent dispersed leaflets of Sapindophylls. Dissected leaves with palmate organization, cf. *Halyserites* Sternberg and *Cussoniophyllum* Velenovsky, are excluded from the Sapindophylls and have not been observed in the NRM region.

Sapindophylls are an important component of many North American Albian and Cenomanian floras (Berry, 1922a, 1922b; Fontaine, 1889; Hickey & Doyle, 1977; Lesquereux, 1874, 1883, 1892; MacNeal, 1958; Upchurch, 1984b). The morphotype is generally considered to be more abundant in floras from regions to the south of the NRM region and is sometimes regarded as representing thermophilous plants. Nonetheless,

the morphotype is common in mid-latitude floras from the NRM region and Greenland (Seward & Conway, 1935), and occurs in southern Alaska ("*Ficus*" *daphnogenoides* in Hollick & Martin, 1930) and the north slope (pers. obs.).

This morphotype is represented by several species in the NRM region (Table 2). A probable new species of *Sapindopsis* of Middle Albian age is illustrated from rocks equivalent to the Thermopolis Shale in southwestern Montana (Fig. 18). It appears to be related to the Cenomanian species "*Sapindus*" *morrisonii* and "*Ficus*" *beckwithii.* A Sapindophyll similar to *Sapindopsis variabilis* Fontaine is present in the Blackleaf Formation of Montana (Fig. 19). Sapindophylls are present in the Albian of Alberta (Table 2, Fig. 20), British Columbia (Fig. 27), and Washington (Figs. 28–32). A putative Sapindophyll (cf. *Sapindopsis* sp.) from the Upper Albian of Idaho is tentatively assigned to this morphotype (Figs. 21–23). This species is allied to the morphotype by admedial orientation of the tertiary veins (Fig. 21) and dissected leaves with decurrent leaflets (Figs. 22, 23), but shows the irregular laminar furcations of *Halyserites.*

Sapindophylls may be most closely allied to Recent basal Saxifragales and to other rosid groups such as the Sapindales and Rutales. This relationship is based on the pinnately compound leaves, eucamptodromous venation, admedial orientation of the transverse tertiary veins (Hickey & Doyle, 1977), cunonioid teeth in some species (Upchurch, 1984b), and cuticular features (Upchurch, 1984b). Crane et al. (1986) discussed possible relationships between Sapindophylls and Platanophylls in the context of the Late Albian radiation of dicotyledons that produced tricolpate pollen (viz. Hamamelididae and

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FIGURES 5–58. Representative dicotyledonous leaves from the Albian through middle Campanian of the NRM region. All figures with centimeter scales. Specimens from the U.S. National Museum are provided with USGS field locality numbers, and those from the Geological Survey of Canada are provided with GSC locality numbers. Types and other cataloged specimens are indicated where appropriate, along with U.S. National Museum (USNM) and Geological Survey of Canada (GSC) accession numbers. Names applied to illustrated specimens are as originally published or as identified in paleobotanical collections at the USNM and GSC. I have provided names only for species from the Fall River, Blackleaf, Pre-Muddy, Pasayten, Mowry, Winthrop, and Two Medicine floras.

FIGURES 5–12. Albian age dicotyledonous leaves of the Pentalobaphyll and Platanophyll morphotypes. 5–9. Pentalobaphylls.—5. cf. "*Sterculia*" *mucronata* Lesquereux, Fall River Formation, USGS locality 7404. 6–8. *Araliaephyllum westonii* (Dawson) Bell.—6. Blackleaf Formation, USGS locality 9439. 7, 8. Mill Creek Formation.—7. GSC locality 1815, GSC 5117, holotype.—8. GSC locality 3066, GSC 5874.—9. "*Aralia*" *rotundata* Dawson, Mill Creek Formation, GSC locality 1815, GSC 5116, holotype. 10–12. Platanophylls.—10. "*Platanus*" sp., Mill Creek Formation, GSC locality 1815, GSC 5106.—11. *Platanophyllum* sp., Blackleaf Formation, USGS locality 9437.—12. cf. *Aspidophyllum trilobatum* Lesquereux, Blackleaf Formation, USGS locality 9437.
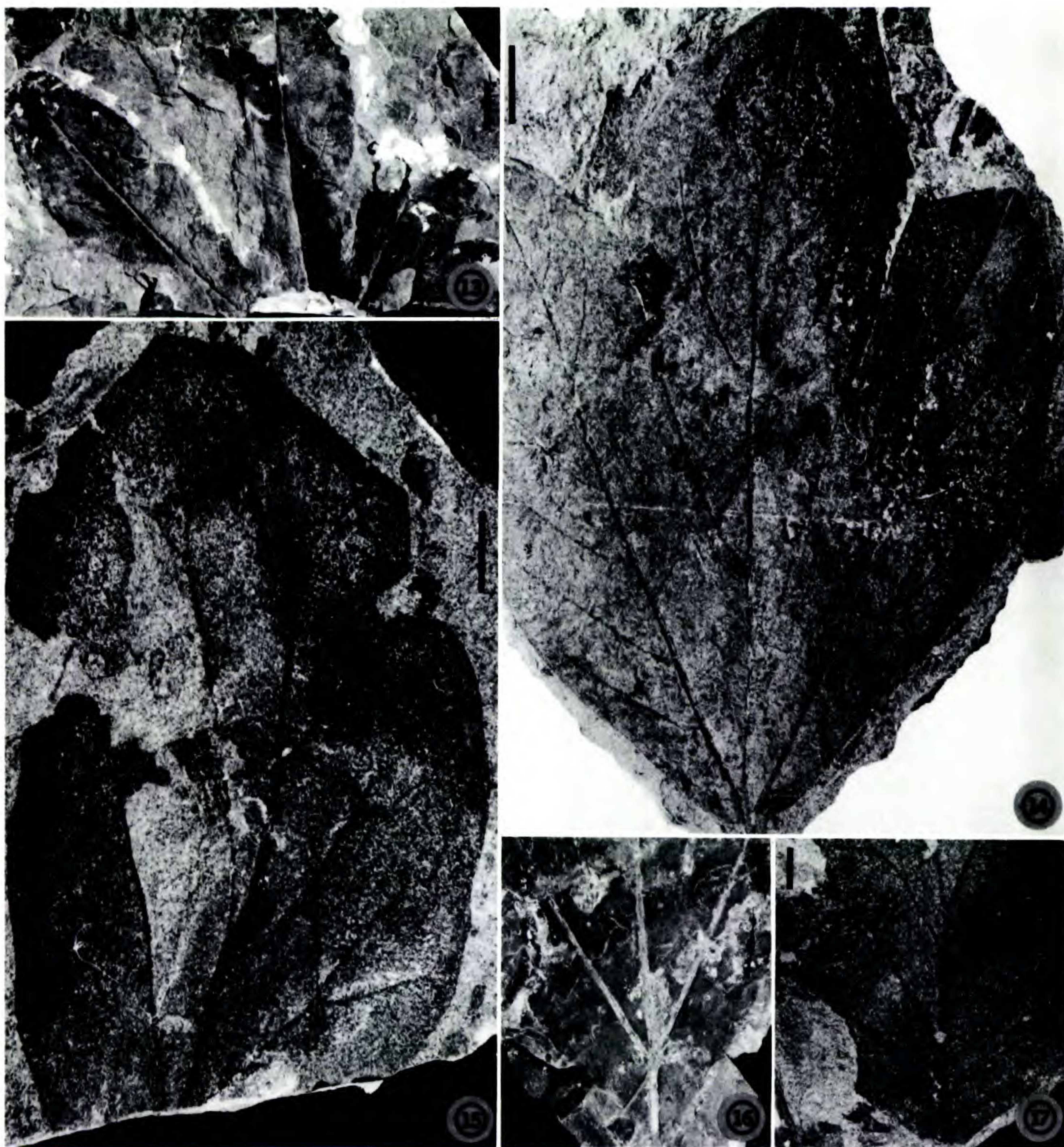
FIGURES 13–17. Albian age dicotyledonous leaves of the Platanophyll and Protophyll morphotypes. 13, 14. Platanophylls.—13. cf. "*Aralia*" *wellingtoniana* Lesquereux, Blackleaf Formation, USGS locality 5984.—14. *Araliopsoides* cf. *cretacea* (Newberry) Berry, Blackleaf Formation. 15. Protophyll, cf. *Protophyllum* sp., Blackleaf Formation, USGS locality 5986. 16, 17. Comparison of basal venation of Platanophyll and Protophyll.—16. Platanophyll, *Platanophyllum* sp., Blackleaf Formation, USGS locality 5939.—17. Protophyll, *Protophyllum* sp., Blackleaf Formation, USGS locality 5986.

Rosidae). Friis & Skarby (1982) and Basinger & Dilcher (1984) discussed Cretaceous flowers and pollen of early Rosidae.

Sapindophylls are restricted to Albian and Cenomanian floras in the NRM region. I am not familiar with their Late Cretaceous range elsewhere. The rosid affinities of Sapindophylls need to be confirmed by further study, as does the relationship between the group and the putative

Upper Cretaceous and Paleocene derivative *Averhoites.*

Trochodendrophyll. Leaves simple, ovate to reniform. Margin crenate. Teeth convex-convex (A–1), chloranthoid. Venation actinodromous. Primary veins usually 3 or 5, sometimes more, arched apically. Secondary venation semicraspedodromous with ± prominent brochidodro-

mous arches present apically. Tertiary and higher order venation not well known, appearing reticulate in some with tendency towards orthogonal branching.

This group is characterized by actinodromous primary venation and crenate margins bearing chloranthoid teeth (Fig. 4). The latter character distinguishes the group from those Menispermaphylls with actinodromous venation. Trochodendrophylls are reported in low frequencies during the Albian, and are represented in the NRM region primarily from Alberta and British Columbia (Table 2). *Trochodendroides* ("*Cercidiphyllum*") *potomacensis* (Ward) Bell conforms most closely to the concept of the morphotype with five primary veins, brochidodromous secondary veins, and crenate margin (Figs. 24, 25).

Trochodendrophylls have been assigned to rather unlikely genera (Table 1). Cuticular studies of *Menispermites potomacensis* Berry from the Lower Cretaceous Potomac Group (Upchurch, 1984b; pers. comm.) indicate that the stomatal structure of this species does not conform to that of extant Cercidiphyllales and Trochodendrales. Probable members of the lineage are reported in high frequencies from Senonian and latest Cretaceous deposits, but these are more advanced in morphology and in some cases can be appropriately assigned to the Recent Trochodendraceae and Cercidiphyllaceae (see Krassilov, 1973b). Trochodendrophylls, along with a series of pinnately veined Lower Cretaceous leaves with chloranthoid teeth and open craspedodromous secondaries (see Upchurch, 1984b; Fig. 36, this report), may represent an ancestral plexus from which Recent Trochodendrales and Cercidiphyllales evolved during the Cretaceous (but see Wolfe, 1973). The Campanian Two Medicine flora (see below) includes four leaf taxa which have chloranthoid teeth, but which exhibit variations of primary and higher order venation that suggest mosaic development of leaf characters in Cercidiphyllales, Trochodendrales, and Chloranthales.

Menispermaphyll. Leaves apparently simple, broadly deltoid and ± trilobed to circular or ovate-elliptic. Base cordate to obtuse. Margins entire or lobate forms occasionally with teeth. Venation acrodromous or actinodromous with 3–9 primary veins. Primary veins craspedodrome or becoming camptodrome just before margin. Secondary veins irregularly spaced, camptodrome in many but craspedodrome to the

teeth in nonentire forms. Tertiary veins random-reticulate to transverse. Higher order venation not observed. Cuticle unknown.

This group (Fig. 4) superficially resembles Nymphaeaphylls but is never peltate and never has an expanded, multistranded petiole. Cordate leaves with major veins unbranched to the margin are best placed in Menispermaphylls, whereas such leaves with highly branched primary and secondary veins are more appropriately placed in Nymphaeaphylls. Trochodendrophylls may be distinguished by their crenate margin.

Menispermaphylls are morphologically convergent with extant Menispermaceae (Ranunculiidae). The modern family includes both simple-leaved and ternately compound members. The leaves and leaflets are deltoid to ovate with entire or sparingly toothed margins. Tooth morphology is a modification of the chloranthoid type (Hickey & Wolfe, 1975). Primary venation is actinodromous or acrodromous, and major veins terminate in a fimbrial vein, thus appearing craspedodromous. Many Recent species exhibit a mucronate leaf apex; simple, unbranched trichomes; and well-developed, orthogonal-reticulate, higher order venation.

Menispermaphylls resemble Recent Menispermaceae in shape, margin, and venation. However, before relationship to the family can be established it is necessary to demonstrate the presence in the fossils of such characters as fimbrial veins and simple, unbranched trichomes. Nevertheless, the unusual combination of entire margin and craspedodrome primary veins is an important point of agreement between the fossils and Recent Menispermaceae.

Menispermaphylls show their greatest diversity in the Dakota flora of Kansas and Nebraska (Lesquereux, 1892). However, here, as in the NRM region (Table 2), they are a relatively minor component of the flora. The Campanian Two Medicine flora (see below) includes a species that is entirely consistent with the leaf morphology of extant Menispermaceae.

Magnoliaephyll. Leaves simple, ovate to elliptical. Margin entire or 2- or 3-lobed. Primary venation pinnate in entire forms, with 3 primary veins from base in lobed forms. Secondary venation brochidodromous or festooned brochidodromous. Higher order venation variable.

This morphotype (Table 1) comprises a large number of problematic taxa that form an im-

portant part of all but extreme northern Laurasian floras. The group is erected primarily for convenience due to the enigmatic positions of most of its members. Some Potomac Group Magnoliaephylls for which cuticular evidence is available (Upchurch, 1984a, 1984b) appear to be related to Laurales and Illiciales. "*Magnolia*" *magnifica* Dawson is illustrated as an example of the morphotype (Fig. 26). Early members of the morphotype from the NRM region are listed in Table 2.
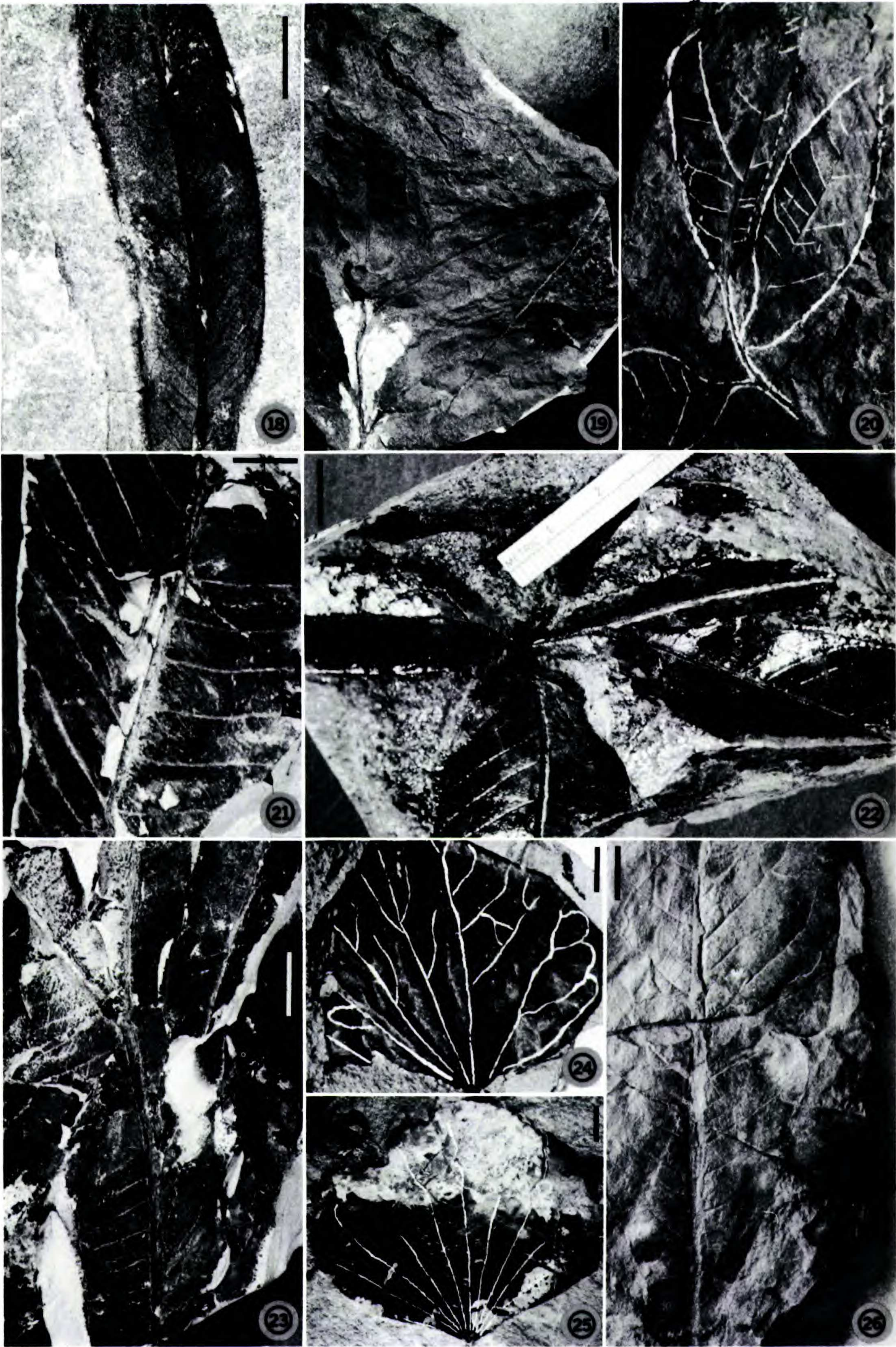
Putative magnoliid infructescences are known from the mid Cretaceous of central North America (Dilcher, 1979), Japan (Nishida, 1985), and Greenland (Seward & Conway, 1935). Walker et al. (1983) reported pollen of Winteraceae from the Lower Cretaceous of Israel.

Cinnamomophyll. Leaves simple. Margin entire. Venation pinnate. Prominent suprabasal secondary veins arching apically. Secondary venation brochidodromous. Basilaminar secondary veins sometimes present. Tertiary veins transverse, regular or somewhat irregular in spacing and course. Quaternary veins weak, random-reticulate. Cuticle unknown.

This morphotype (Fig. 4) is widely reported from NRM region floras and is an important component of the angiosperm vegetation during the Albian (Table 2). Although not present in all Cinnamomophylls, basilaminar secondary veins indicate that some may be related to extant Laurales. Cinnamomophylls are most important in floras from middle latitudes in Laurasia where they are consistently represented in the Albian floras.

Nymphaeaphyll. Leaves simple, orbicular to reniform. Margin entire. Petiole often multistranded. Base cordate or peltate. Venation actinodromous or pinnate with strong lateral veins radiating from a congested base. Primary and secondary veins branching ± equally. Marginal venation forming weak brochidodromous arch-

es, craspedodromous in "*Castalia*" and *Castaliites*. Cuticle unknown.

This morphotype converges with Trochodendrophylls, from which it is distinguished by its entire margin, and with Menispermaphylls (see discussion of Menispermaphylls and Fig. 4).

Several species of Nymphaeaphylls exhibit leaf architecture consistent with those of extant Nymphaeales and Nelumbonales. Evidence from cuticles and fruits is needed to confirm the relationship.

Cordate and peltate leaves with actinodromous venation and entire margins are abundant and diverse in the North American mid Cretaceous, but they are not well represented in the NRM flora (Table 2). Nymphaeaphylls may represent an adaptational syndrome for aquatic habitats as suggested by Samylina (1968), Axelrod (1970), and Krassilov (1977). Hughes (1976) suggested that this leaf morphology may represent simply an early "experimental" shape that is not correlated with aquatic habitats.

Rhamnophyll. Leaves simple. Margin entire or crenate-dentate. Base acute to truncate. Venation acrodromous. Primary veins 3–5, arising from within the petiole and arching apically. Secondary venation brochidodromous or semicraspedodromous to teeth, often with several regular and prominent secondary veins originating on outermost primary veins and arching apically along margins. Tertiary veins transverse, regularly spaced and usually numerous. Higher order venation not observed. Cuticle unknown.

Rhamnophylls are rare from floras of Albian age in the NRM region (Table 2). The group occurs with greater frequency in Late Cretaceous floras throughout western North America (Hickey, 1984). Rhamnophylls can be distinguished from Cinnamomophylls (Fig. 4) by the petiolar divergence of the acrodromous primary veins and by the presence of teeth in some. The botanical affinities of the former remain unknown.

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FIGURES 18–26. Albian age dicotyledonous leaves of the Sapindophyll, Trochodendrophyll, and Magnoliaephyll morphotypes. 18–23. Sapindophylls.—18. cf. "*Rhus*" *powelliana* Lesquereux, Pre-Muddy collection.— 19. cf. *Sapindopsis* sp., Blackleaf Formation, USGS locality 6007.—20. *Fontainea grandifolia* Newberry, Commotion Formation, GSC locality 3204, hypotype (as labeled in GSC collections), GSC 6639. 21–23. cf. *Sapindopsis* sp., Wayan Formation. 24–25. Trochodendrophylls, *Trochodendroides* ("*Cercidiphyllum*") *potomacensis* (Ward) Bell, Kingsvale Formation.—24. GSC locality 3449, GSC 6654.—25. GSC locality 3125, GSC 5907.— 26. Magnoliaephylls, "*Magnolia*" *magnifica* Dawson, GSC locality 290, GSC 5133, holotype.

Cornophyll. Leaves simple. Margin entire. Primary venation pinnate. Secondary venation camptodromous, arching apically. Tertiary veins transverse, regularly spaced, more or less numerous. Higher order venation and cuticle unknown.

Cornophylls occur in limited diversity and abundance in the Albian floras of the region (Table 2). The group assumes a more important position in later Cretaceous floras. The botanical affinity of the group is unknown, but some members appear to exhibit morphological similarities to Rosidae.

Dryophyll. Leaves palmately compound. Leaflets ovate to lanceolate. Margin serrate. Primary venation pinnate. Secondary venation craspedodromous. Higher order venation not observed. Cuticle in Krassilov (1973b) and Němejc & Kvaček (1975).

This group of palmately compound leaves with serrate margins is not present in the early angiosperm floras. They appear first in the uppermost Albian and Cenomanian. Serrate forms with craspedodromous venation and lanceolate leaflets (cf. *Dryophyllum* Debey) can be shown to share morphological similarities with Fagales, although this is a tenuous association for most Cretaceous forms (Wolfe, 1973).

FLORISTIC PROVINCIALITY OF THE NORTHERN ROCKY MOUNTAIN REGION DURING THE ALBIAN

Discussion of floristic provinciality during the Cretaceous ultimately depends on accurate correlation of stage and substage boundaries between the proposed provinces. The Upper–Lower Cretaceous boundary and the position of the Albian substages in the NRM region are placed based on ammonites in the United States (Cobban & Reeside, 1951, 1952a) and on a varied molluscan fauna in Canada (Jeletsky, 1968; Kauffman, 1975). Geologists have generally placed the boundary between the Upper and Lower Cretaceous in the NRM region at the top of the Mowry Shale. This boundary coincides with the uppermost widespread occurrence of *Neogastroplites* (Cobban & Reeside, 1951). It also coincides with the first occurrence of tricolporate pollen in the region (Nichols et al., 1983; Norris et al., 1975). Nonetheless, uncertainty exists over the correlation of the regional boundary to the European standard. The boundary in the western

interior is radiometrically dated as 94 Ma (Obradovich & Cobban, 1975; but also see Fouch et al., 1983), whereas in Europe it is dated as 97.5 Ma (Harland et al., 1982).

Brenner (1976) recognized a Northern Laurasian Province and a Southern Laurasian Province based on the palynology of Lower Cretaceous deposits. The northern province is recognized by a coniferous palynoflora less diverse and more heavily bisaccate than the southern province. The NRM region lies on the boundary between provinces. Such provinciality is supported by Srivastava (1981) and by Hickey & Doyle (1977) and rejected by Herngreen & Chlonova (1981). Angiosperm pollen has been used for the recognition of Late Cretaceous provinciality (Srivastava, 1981). The extension of angiosperm palynofloral provinces into the Early Cretaceous seems reasonable in light of the elaboration of the timing of the migration of angiosperms provided by Brenner (1976) and by Hickey & Doyle (1977).

The poleward migration of early angiosperms was first recognized from megafossils (Axelrod, 1959) and subsequently refined through palynological studies (Brenner, 1976; Hickey & Doyle, 1977). Early angiosperms appear to have arisen in northern Gondwana and to have crossed the Tethys into Laurasia in the Late Barremian and Aptian (Hickey & Doyle, 1977). Entry of monosulcate-producing angiosperms into northern latitudes of Laurasia was delayed by several million years. This may be attributed to climatic or other environmental barriers, inadequate dispersal mechanisms, or merely to stalwart pre-existing vegetation. Tricolpate taxa exhibit a far shorter lag period. The first major radiation of the tricolpate group occurs on a worldwide scale during the late Middle Albian (excepting at the very highest latitudes).

Considerations of floral provinciality of early angiosperms must address two common problems with palynological investigations: 1) underspeciation, i.e., approximate equivalency of a palynological species with a natural genus (Muller, 1970; Tschudy & Tschudy, 1986), especially in the Paleozoic and Mesozoic, and 2) spurious conspecificity, i.e., the tendency to assign pollen grains to existing taxa. Both problems obscure provincialism at lower taxonomic levels. Penny (1969) commented on the impoverished appearance of Cenomanian pollen floras relative to leaf floras of that age. A related problem, which is more or less confined to the early angiosperm

pollen floras, is the general absence of differentiation of grains with respect to ornamentation, shape, and gross morphology. In addition, Mesozoic palynologists do not normally elaborate species frequency as is common for Holocene workers, a situation that makes it difficult to review existing literature for data which could be used to determine provinciality based on dominance and importance of species. On the other hand, a common problem with megafloral taxonomy has been overspeciation due to failure to recognize physiognomic variation in leaf morphology within natural species. Both megafloral and microfloral treatments are restricted by the taphonomic biases implicit in any depositional environment.

The first angiosperms known from the lower Middle Albian (Potomac subzone IIB) of the NRM region are two grains of *Tricolpites micromunus* (Groot & Penny) Singh from the upper Loon River Formation in northwest Alberta (Singh, 1971) and monosulcate grains from the Cloverly Formation in Wyoming (Davis, 1963). Pollen and megafossils are known throughout the NRM region with certainty from the middle Middle Albian (Bell, 1956; Davis, 1963; Nichols & Jacobson, 1982; Norris, 1967; Singh, 1975; Roberts, 1972). Singh (1971) reported nine species of middle Middle Albian angiosperm pollen from northwest Alberta. By upper Middle Albian (Potomac subzone IIB), angiosperm pollen becomes a persistent element of moderate frequency in the microflora. This upper Middle Albian surge in frequency seems to be common to most of North America other than far northern latitudes.

The first angiosperm megafossil from the region, *Sapindopsis angusta* (Heer) Seward, occurs in the lower Middle Albian (Potomac subzone IIB). Localities in British Columbia of equal age yield *Sapindopsis* and a limited diversity of other dicot leaves (Table 2). The first diverse assemblages of megafossils are of middle Middle and upper Middle Albian age and include Sapindophylls, Pentalobaphylls, Platanophylls, *Cinnamomoides, Trochodendroides,* and *Menispermites* in order of frequency in collections. The components of this megaflora continue into the lower Upper Albian with little apparent change. The early angiosperm flora of the region is distinct from more southerly floras in its high representation of Pentalobaphylls, Cinnamomophylls, and to a lesser degree *Trochodendroides,* and several endemic species are present.

I compared the Lower Cretaceous palynoflora of the Patapsco Formation of Maryland (Brenner, 1963) with that of the Loon River and Peace River formations of northwest Alberta (Singh, 1971) to contrast composition, abundance, and diversity of Middle and Late Albian floras of eastern North America with those of the NRM region. More recent treatments of the Patapsco palynoflora exist (Doyle, 1969; Doyle & Hickey, 1976; Hickey & Doyle, 1977), but Brenner's work remains the standard for taxonomic comparison in the absence of a revision. Brenner apparently was conservative in recognition of taxa, thus it is likely that some of his taxa represent species complexes or genera.

Monosulcates first occur in the latest Barremian or early Aptian in eastern floras, considerably antedating their lower Middle Albian occurrence in the NRM region. Seven of the twelve Patapsco species of angiosperm pollen are tricolpate. The tricolpates appear during the Lower and Middle Albian and continue upsection to the top of the formation (middle Upper Albian) with no addition of new species (Brenner, 1963; but also see Doyle & Hickey, 1976). Of these seven species, *Tricolpites micromunus* occurs in the lower Middle Albian Loon River Formation, and six of the seven tricolpates occur in the middle Middle Albian Harmon Member of the Peace River Formation. Such palynological data indicate close similarity between lower and middle Middle Albian dicots in the eastern and western floras of North America, at least at the generic level.

An endemic flora in the region is indicated by angiosperm pollen recovered from the Peace River Group (Singh, 1971), which was deposited during and after the maximum transgression of the middle Albian seaway. Nineteen species comprise the angiosperm palynoflora in the upper Middle Albian Cadotte Member of the Peace River Formation. Nine of these, including five tricolpates, are reported from the Patapsco, still a high degree of similarity, but strikingly less than that of the earlier flora. Furthermore, five Cadotte taxa have not been reported from Cretaceous palynofloras outside the NRM region. Eastern groups apparently moved north and east into the NRM region during the Middle Albian and persisted in the western flora; however, by the upper Middle Albian, tricolpate and monosulcate taxa indicate endemism in the region. Among the endemics are the monosulcate species *Liliacidites trichotomosulcatus* Singh and the tricolpates *Retitricolpites maximus* Singh, *Tricol-*
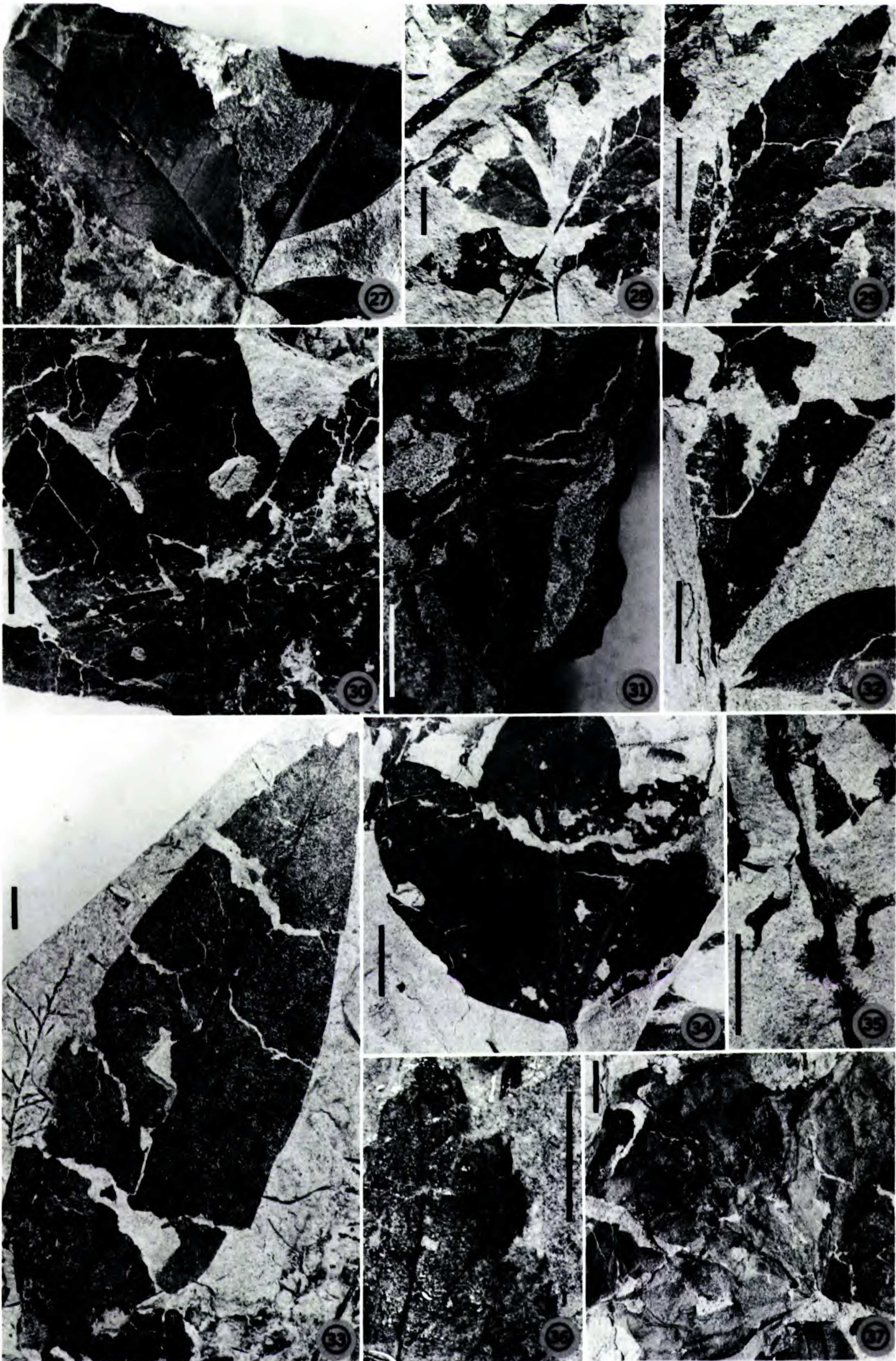
pites sagax Norris, *T. parvus* Stanley, and *Fraxinaipollenites venustus* Singh.

The endemic character of the flora appears to result largely from separation of the region from eastern North America by the Skull Creek Seaway for approximately two million years during the upper Middle and lower Upper Albian. Thus, shortly after angiosperms entered the region, they were cut off from their presumed ancestral stock to the south and east in an area some 20° further north and potentially subject to substantially different selective pressures. However, it should be noted that available palynofloras make it difficult to resolve an east-to-west adaptive radiation within groups producing small, reticulate, tricolpate pollen, since the equivalence of named species to biological species is debatable. In contrast to the simple tricolpate pollen, leaf architectures and cuticles of Lower Cretaceous angiosperms provide an expanded suite of characters from which biological species can be circumscribed. A detailed comparison of North American floras of Albian age is beyond the scope of this paper.

WINTHROP FLORA

A large collection of fossil foliage from the type locality of the Late Albian or Early Cenomanian (Barksdale, 1975) Winthrop Formation in central Washington (Figs. 1, 2) appears to be the latest occurring "archaic" flora in the region. The flora contains abundant Sapindophylls and Pentalobaphylls that are closely related to but not conspecific with those of earlier Albian floras from the NRM region.

Several small collections of plant fossils from the Winthrop have appeared as floral lists in geological papers (see Barksdale, 1975). Apparently the collections were sent to the U.S. National Museum and examined by F. Knowlton and R. Brown. Reevaluation of these collections in 1986 by S. Wing and J. Wolfe (pers. comm.) indicated a Paleocene age for the flora, and hence their origin in the Winthrop Formation must be questioned. The present report includes only those specimens collected from the type locality (Appendix I) by R. Rau, J. Robison, and myself.

The Winthrop flora is a moderately diverse assemblage consisting of about 20 species of ferns, conifers, dicotyledons, and *Sagenopteris* (Caytoniales). Dicotyledonous species include *Sapindopsis* sp. (Figs. 28–32), *Magnoliaephyllum* sp. (Fig. 33), *Araliaephyllum* sp. (Fig. 34), *Araliaephyllum westonii*, "*Sparganium*" sp. (Fig. 35), an unidentified dicot with craspedodromous secondary venation and chloranthoid teeth (Fig. 36), *Nelumbites* sp. (Fig. 37), "*Ficus*" *ovalifolia*, *Menispermites* sp., *Eucalyptophyllum* sp., and several poorly preserved species.

UPPERMOST ALBIAN, CENOMANIAN, AND TURONIAN FLORAS

Three well-developed floras, the Aspen, Frontier, and Dunvegan (Table 3), provide much of the megafossil evidence for the angiosperm flora of the NRM region during the uppermost Albian and Cenomanian (Fig. 2). The Dunvegan flora is near the northern limit of the region; the Aspen and Frontier are at the southern limit (Fig. 1). Collections from the Albino Member of the Mowry Formation and the Wayan Formation (Figs. 1, 2) provide a few additional species.

The Albian angiosperm flora of the region shows an underlying unity due to the occurrence in most assemblages of Sapindophylls, Pentalobaphylls, Platanophylls, Protophylls, and Cinnamomophylls, which give the flora an "archaic" appearance when contrasted to the flora of the post-Albian. The post-Albian flora shows the development of north–south provinciality in the region. However, because of the small number of floras known from this period (Fig. 2), and the restricted volcaniclastic facies of the Aspen and Frontier floras, such provinciality is at this time somewhat conjectural. Moreover, because the early angiosperm flora is known primarily from deposits in the northern half of the region, there is uncertainty over how widespread and uniform the early flora was.

The development of intraregional provincial-

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FIGURES 27–37. Dicotyledonous leaves from the Pasayten and Winthrop formations. 27. Pasayten Formation, *Sapindopsis* sp. 28–37. Winthrop Formation. 28–32. *Sapindopsis* sp.—28. Upper part of compound leaf.—29. Enlarged leaflet of specimen in Figure 28.—30. Upper part of compound leaf.—31. Base of leaf.—32. Base of joined upper three leaflets.—33. *Magnoliaephyllum* sp.—34. *Araliaephyllum* sp.—35. "*Sparganium*" sp.—36. Unidentified leaf with craspedodrome secondaries and chloranthoid teeth.—37. *Nelumbites* sp.

TABLE 3. Angiosperm flora from the uppermost Albian, Cenomanian and Turonian of the northern Rocky Mountain region.[1,2,3]

	Aspen (2)	Lower Frontier (11a)	Dunvegan (8) A	Dunvegan (8) B	Upper Frontier (11b)
Sapindophyll					
"Andromeda"? spatula Bell				X	
"Ficus" daphnogenoides (Heer) Berry				X	
"Myrica" nervosa Knowlton		X			
Sapindopsis schultzii Brown	X				
Rosidlike Leaves					
"Diospyros" nitida Dawson			X		
"Hymenaea" fayettensis Berry				X	
"Laurus" aspensis Brown	X				
Phyllites dentata Knowlton		X			
"Prunus" aspensis Brown	X				
"Salix" cumberlandensis Knowlton		X			
"Staphylea"? fremontii Knowlton	X	X			
Platanophyll					
Ampelophyllites attenuatus (Lesquereux) Knowlton				X	
"Aralia" cf. parvidens Hollick				X	
"Aralia" veatchii Knowlton		X			
Aspidophyllum dentatum? Lesquereux				X	
"Hedera" cf. cretacea Lesquereux				X	
"Platanus" latiloba Newberry				X	
Pseudoaspidophyllum latifolium Hollick				X	
"Quercus" stantonii Knowlton		X			
"Sparganium" aspensis Brown	X				
Protophyll					
Credneria macrophylla Heer				X	
Credneria truncatodenticulata Bell				X	
"Platanus" affinis Lesquereux				X	
"Platanus" williamsii Bell				X	
Populites cyclophylla Dawson			X		
Protophyllum boreale Dawson			X		
Protophyllum leconteanum? Dawson			X		
Protophyllum multinerve? Lesquereux				X	
Protophyllum rugosum Lesquereux			X		
Pseudoprotophyllum boreale (Dawson) Hollick				X	
Pentalobaphyll					
Araliaephyllum rotundiloba (Newberry) Fritel				X	
Araliaephyllum groenlandica? Heer				X	
"Sterculia" towneri (Lesquereux) Berry					X
Dryophyll					
Dewalquea pulchella Knowlton		X			
Dryandroides lanceolata Knowlton	X	X			
Dryophyllum gracile Debey				X	
Dryophyllum lanceolatum (Knowlton) Berry	X				X
Trochodendrophyll					
Castaliites cf. cordatus Hollick (in part)				X	
Trochodendroides ("Cercidiphyllum") potomacensis (Ward) Berry				X	

TABLE 3. Continued.

	Aspen (2)	Lower Frontier (11a)	Dunvegan (8) A	Dunvegan (8) B	Upper Frontier (11b)
Cinnamomophyll					
"Cinnamomum" heeri Lesquereux				X	
"Cinnamomum" hesperium Knowlton		X			
"Cinnamomum" sp.		X			
Phyllites sp.		X			
Nymphaeaphyll					
Castaliites cf. cordatus (in part)				X	
Menispermites reniformis Dawson			X	X	
"Nelumbo" weymouthii Brown	X				
Nymphaeites exemplaris Hollick				X	
Paleonuphar nordenskioldii (Heer) Bell				X	
Magnoliaephyll					
"Ficus" maxima Dawson			X		
"Liriodendron" giganteum Lesquereux				X	
"Magnolia" boulayana Lesquereux				X	
"Magnolia" hollickii Berry				X	
"Magnolia" lacoeana Lesquereux				X	
"Magnolia" magnifica Dawson			X	X	
"Magnolia" cf. rotundifolia Newberry				X	
"Magnolia" tenuifolia Dawson			X		
"Sassafras" bradleyi Brown	X				
Cornophyll					
"Diospyros" lesquereuxii Knowlton & Cockerell				X	
"Ficus" fremontii Knowlton		X			X
Laurophyllum debile Dawson			X		
"Magnolia" rhamnoides Bell				X	
Monocots					
Sabalites sp.					X
Uncertain					
"Bauhinia"? cretacea? Newberry				X	
"Dalbergia" hyperborea Heer				X	
Dicotylophyllum sp. A. Bell				X	
"Fagus" protonucifera Dawson			X		
"Ficus" glascoeana Lesquereux				X	
"Ficus" inaequalis Lesquereux					X
"Ficus"? sp.				X	
"Ficus" sp.		X			X
Laurophyllum flexuosum (Newberry) Bell				X	
Leguminosites spatulatus Bell				X	

[1] Numbers in parentheses refer to geographic and stratigraphic position of floras as indicated in Figures 1 and 2.

[2] All species are included as originally cited in the references given below.

[3] Vertical rows indicate single floristic references as follows: (2)—Brown, 1933a. (11a)—Knowlton, 1917. (8)A—Dawson, 1883. (8)B—Bell, 1963. (11b)—Berry, 1929d.

ity in the uppermost Albian and Cenomanian is correlated with the ebb of the Albian epeiric seaway. As previously discussed, the seaway may have influenced the development of endemism in the flora by restricting movement of eastern species into the region during much of the Upper Albian. As the seaway withdrew towards the north at the end of the Albian, immigration from east-

ern and southern regions may have altered the floristics of the southern part of the NRM region. Although this scenario is hypothetical, the uppermost Albian and Cenomanian floras of Wyoming contain *Dewalquea,* a genus characteristic of floras to the south and east of the region.
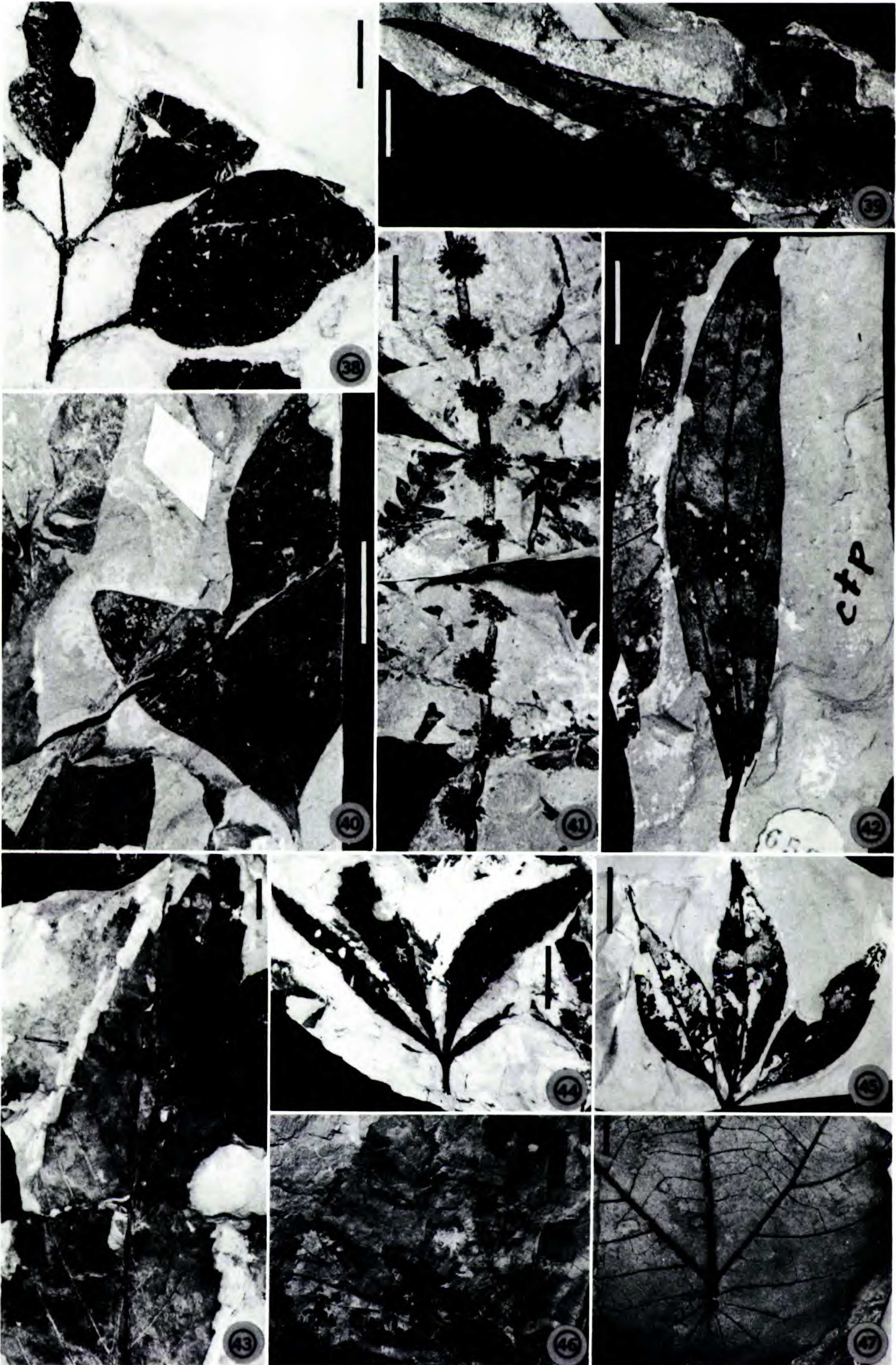
A large collection of fossil leaves from the Wayan Formation in southeast Idaho (Figs. 1, 2) is dominated by pteridophytes (Crabtree, 1983) that are undescribed but appear to be similar to those from the Frontier Formation in southwest Wyoming (Knowlton, 1917). The Wayan contains a single angiosperm, cf. *Sapindopsis* sp. (Figs. 21–23), which appears to be a new species. Andrews (1948) and Andrews & Kern (1947) described a large collection of pteridophytic petrifactions (*Tempskya*) from the Wayan (Appendix I).

Another undescribed megaflora is known from several localities in the Albino Member of the Mowry Formation in southern Montana (Figs. 1, 2, Appendix I). An extensive fern community is preserved in the deltaic deposits of the Albino (Vuke, 1982; Crabtree, 1983). Dicot leaf mats have been excavated at one locality in the Albino (Appendix I). Unfortunately, work on these fossils is incomplete and the floristics of this site remain poorly known. Figure 38 shows a specimen from the Albino that appears to be a pinnately compound leaf, possibly of rosid affinity, but the venation is too poorly preserved to confirm such a determination.

The uppermost Albian Aspen flora (Brown, 1933a, 1933b) from southwest Wyoming (Figs. 1, 2, Table 3) comprises nine species of angiosperms. No species from the Aspen are known from the older floras of the region, although some are recorded from the nearby and slightly younger Frontier Formation (Table 3). Notable in the flora is "*Liquidambar*" *fontanella* Brown (Fig. 39), which possesses glandular teeth similar to those of Recent *Liquidambar* and *Altingia.* "*Sassafras*" *bradleyi* Brown (Fig. 40) is preserved in a semicoalified state, which makes higher order

venation difficult to distinguish. This species shows smooth-margined, palinactinodromous leaves with three lobes such as in extant Lauraceae and certain palmate Dilleniid families. "*Sparganium*" *aspensis* Brown (Fig. 41) is believed to be a Hamamelid fructification. Such fossils are most commonly attributed to Platanoids; however, associated leaves of this form are not present in the Aspen. It is possible that the fructification was produced by *Liquidambar fontanella.* An advanced Sapindophyll, *Sapindopsis schultzii* Brown, is present in the Aspen, as well as several other species of putative rosid affinity (Table 3).

The Cenomanian flora from the Frontier Formation of southwest Wyoming (Hall, 1845; Knowlton, 1917; Andrews & Pearsall, 1941) is a mixed pteridophyte–angiosperm assemblage preserved in volcanic sediments similar to those which yield the Aspen and Albino floras. The flora is from the lowermost part of the Frontier Formation and is referred to as the Lower Frontier flora in Figures 1 and 2 and in Table 3.

"*Cinnamomum*" *hesperium* Knowlton (Fig. 42) is very similar to Cinnamomophylls from the Middle and Late Albian, and as such is the only archaic element in this flora. Platanophylls are represented by "*Aralia*" *veatchii* Knowlton (Fig. 43), which is advanced over earlier members of the morphotype by its deeply divided lamina. *Dewalquea pulchella* Knowlton (Fig. 44) is a toothed, palmately compound leaf of uncertain affinity. The entire-margined, palmately compound leaf of "*Staphylea*"? *fremontii* Knowlton (Fig. 45), which also occurs in the Aspen flora (Table 3), shows well-developed, eucamptodromous secondary venation such as characterized many Rosidae. Palmately compound leaves are restricted to extant Ranunculiidae, Rosidae, and palmate Dilleniidae. Species with and without entire margins can be found in each of these groups. More detailed analysis of the venation and tooth morphology of the palmately compound leaves from the mid Creta-

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FIGURES 38–47. Dicotyledonous leaves from the Mowry, Aspen, Frontier, and Dunvegan formations. 38. Pinnately compound leaf, Mowry Formation. 39–41. Aspen Formation, USGS locality 8169.—39. "*Liquidambar*" *fontanella* Brown, USNM 39146, holotype.—40. "*Sassafras*" *bradleyi* Brown, USNM 39144, holotype.—41. "*Sparganium*" *aspensis* Brown, USNM 39140A, holotype. 42–47. Frontier Formation.—42. "*Cinnamomum*" *hesperium* Knowlton, USGS locality 6527, USNM 35260, holotype. 43–45. USGS locality 5049.—43. "*Aralia*" *veatchii* Knowlton, portion of palmately divided leaf, USNM 35258, holotype.—44. *Dewalquea pulchella* Knowlton, USNM 35255, holotype.—45. "*Staphylea*"? *fremontii* Knowlton, USNM 35230, holotype. 46, 47. Dunvegan Formation.—46. *Pseudoaspidophyllum latifolia* Hollick, GSC locality 4197.—47. *Protophyllum boreale* Dawson, GSC locality 4205, GSC 5398, holotype.

ceous of the region (*Dewalquea pulchella*, "*Dios-pyros*" *nitida* Dawson = "*Hymenaea*" *fayettensis* Berry, *Dryophyllum gracile* Debey, *D. lanceo-latum* (Knowlton) Berry, and "*Staphylea*"? *fre-montii*) is necessary before further conclusions are possible.

Far to the north of the floras just mentioned, the Dunvegan flora (Figs. 1, 2; Dawson, 1883; Bell, 1963, 1965) was recovered from coarse flu-vial deposits in marked contrast to the volcan-iclastic southern deposits. The Dunvegan flora, unlike the more southerly floras, contains several leaf genera that indicate considerable affinity with early angiosperm floras (*Araliaephyllum, Tro-chodendroides,* and "*Cinnamomum*"), as well as new forms. Platanophylls (Fig. 46) and Proto-phylls (Fig. 47) are numerically dominant in the Dunvegan assemblage. Entire-margined, pal-mately compound leaves and Dryophylls relate this flora to the Frontier and Aspen floras. The Dunvegan flora contains a suite of large, entire-margined leaves of the Magnoliaephyll morpho-type (Table 3).

The Turonian flora (Berry, 1929d) from the upper part of the Frontier Formation (Table 3, Appendix I) comprises cycadophytes, taxodia-ceous conifers, Cornophylls, Pentalobaphylls, and fragments of the laminae of a putative palm to which Berry (1929d) applied the name *Sabalites,* although the specimens lack evidence of costa-palmate morphology. In addition, several ro-sidlike leaves are reported from the upper Fron-tier (Table 3).

SANTONIAN FLORAS

The lower Santonian Badheart flora from northeast British Columbia is notable for an abundance of Trochodendrophylls (*Trochoden-droides arctica* (Heer) Berry and "*Zizyphus*" *mcgregorii* (Bell)). These occur in association with the common Upper Cretaceous araucarian co-nifer *Geinitzia formosa* Heer (Bell, 1963).

LOWER CAMPANIAN FLORAS

The floristic record from this time rivals that for the Albian. Near equivalent floras are known from the Milk River, Eagle, and Two Medicine formations in Alberta and Montana (Figs. 1, 2). Floristics of the individual floras vary within a context of dominant Hamamelididae. Also im-portant are Cornophylls and Rhamnophylls. Some collections contain an abundance of ar-aucarian, taxodiaceous, and cupressaceous fo-liage. The small-leaved aquatic dicot *Quereuxia* (cf. "*Trapa*"? *microphylla* Lesquereux) is found in the Two Medicine. The earliest pinnate palm from the region is present in the Two Medicine.

The woody dicotyledonous flora (Bell, 1963, 1965) of the Milk River Formation in southern Alberta (Figs. 1, 2) is preserved in coarse fluvial sandstones and associated sediments. Unusual is the complete absence of Platanophylls from the flora. Other than Trochodendrophylls, there is an overall dearth of Hamamelidids. Trocho-dendrophylls (*Trochodendroides arctica* and *T. dorfii* Bell), Cornophylls ("*Magnolia*"? *coalvil-lensis* Knowlton and *Celastrinites* sp.), and Rhamnophylls ("*Ficus*" *trinervis* Knowlton) are the most abundant dicotyledonous leaf fossils.

The Eagle Formation extends through most of central Montana and northern Wyoming. A number of fossil localities are known, and some collecting has been done (see Appendix I), but our knowledge of the Eagle flora is based at pres-ent on the work of Knowlton (1900) in central Montana, and Bell (1963) in northcentral Mon-tana. I was not able to locate the original collec-tions for either of these treatments (see Appendix I), so my discussion is based on the published accounts.

Bell (1963) recognized five dicotyledons from the Eagle. The composition of the flora is very similar to that of the Milk River with *Trocho-dendroides dorfii,* Cornophylls, and Rhamno-phylls. In addition, the flora contains a magno-liid-grade leaf "*Ficus*" *missouriensis* Knowlton, which was first described from the Eagle in cen-tral Montana (Knowlton, 1900).

Knowlton (1900) described a small, poorly preserved collection from the banks of the Mis-souri River (Appendix I). The flora contains a Platanophyll ("*Platanus*"? *wardii* Knowlton), which seems to be reliable to the family level. A Rhamnophyll ("*Ficus*" *trinervis*) and a rosid leaf ("*Juglans*" *missouriensis* Knowlton) are present. The latter may be sapindalean or juglandalean, based on the semicraspedodromous secondary veins that terminate near the sinuses of the teeth, margins with rosid teeth and rosidlike sinus brac-ing, and percurrent, transverse tertiary venation. "*Liriodendron*" *alatum* Newberry, a large leaf of probable magnolialean affinity, was also reported by Knowlton (1900). Knowlton's specimen shows little more than secondary venation, and identity with the type from the Amboy Clays (Newberry, 1895) must be considered tentative.

A more extensive, well-preserved assemblage

from the lower Campanian Two Medicine For-
mation in northern Montana (Figs. 1, 2) is cur-
rently under investigation as part of my doctoral
program. The flora consists of about 30 species
of angiosperms, two conifers, and six ferns, and
was recovered in Oilfield Coulee (Appendix I)
from a single fluvial system extending in outcrop
for two kilometers. It records the vegetation along
a coastal plain river.

Pinnate palm fronds (Fig. 37) dominate the
channel margin facies throughout the outcrop.
The fronds are up to two meters long and are
incompletely divided into induplicate segments.
The fossil palm could be assigned to the form
genus *Phoenicites* (sensu Read & Hickey, 1972)
were it not for the absence of spines at the base
of the frond. Occasional interbedded paludal fa-
cies contain "*Trapa*" (*Quereuxia*). Taxodiaceous
and cupressaceous conifers are found in the basal
lag deposits of paludal facies. *Nymphaeites* sp.
foliage occurs in restricted parts of the outcrop.

Levee and other near-channel facies contain a
diverse dicotyledonous flora that is dominated
by leaves of Hamamelididae. Nonhamamelidid
dicot leaves typically comprise about 10% of the
megafossils. Dicot 43 (Fig. 49) is characterized
by coriaceous texture, entire margins, and weakly
percurrent tertiary venation irregularly spaced,
eucamptodromous secondary veins that origi-
nate almost perpendicular to the midvein and
turn upward rather abruptly near the margin.
The leaf morphology indicates closest relation-
ship to extant Rutales but should be considered
tentative since Rutales have pinnately com-
pound leaves, a feature not demonstrated for Di-
cot 43. A putative dilleniid (Dicot 1, Fig. 50)
shows theoid teeth and closely spaced, thin,
transverse-percurrent, tertiary venation. Several
other minor components of the Oilfield Coulee
flora have affinities to Dilleniidae on the basis
of tooth morphology. Two species (Dicots 57 and
19, unfigured) of entire-margined, imperfectly
actinodromous leaves with thin, percurrent, ter-
tiary veins arranged in concentric series relative
to the base of the leaf indicate palmate dilleniids.

A complex of four species (three of which are
illustrated in Figs. 51–53) are related by their
chloranthoid teeth and form an important and
pervasive element at Oilfield Coulee. Dicot 11
(Fig. 51) is pinnately veined with secondary veins
clustered at the base; these are weakly craspe-
dodromous, and the tertiaries are thin and trans-
verse-percurrent. The leaf shows closest affinity
with Trochodendrales but cannot be accom-

modated in either of the extant genera *Trocho-
dendron* or *Tetracentron*. Another leaf in this
complex (Dicot 12, not figured) more closely re-
sembles extant *Trochodendron*, especially in de-
tails of tertiary and quaternary venation. Dicot
53 (Fig. 52) is a small, broadly elliptic leaf with
pinnate venation and with secondary veins clus-
tered at the base. Dicot 53 shares with extant
Cercidiphyllum such features as shape, orienta-
tion and behavior of tertiary and higher order
venation, and chloranthoid teeth with a tripod-
like arrangement of accessory veins. *Cercidi-
phyllum* differs from the fossil in its well-devel-
oped actinodromous venation and greater
tendency for tertiary veins to bifurcate. Dicot 53
is sufficiently like extant *Cercidiphyllum* that it
can be placed into Cercidiphyllales. Dicot 50 (Fig.
53) has pinnate venation, craspedodromous sec-
ondary veins with the basal pair strengthened,
and acute chloranthoid teeth. Tooth morphology
most closely approaches extant Atherosperma-
taceae; however, the craspedodromous second-
aries and strong basal secondary veins of Dicot
50 make it a problematic species intermediate
in morphology between Laurales/Chloranthales
and Trochodendrales.

Dicot 25 (Fig. 54) has a morphology close to
some extant Hamamelidaceae, notably Recent
Fortunearia. The fossil has strong craspedo-
dromous secondary veins that end in scalloped
teeth with spinose tips; the tertiary and quater-
nary venation is strong and branched orthogo-
nally. Dicot 25 is the most abundant and wide-
spread of the Two Medicine dicot taxa and
probably represented a deciduous plant with large,
chartaceous leaves. Another hamamelid (Dicot
36, not figured) shows leaf morphological fea-
tures convergent with extant *Hamamelis* and
Fothergilla. Second in overall abundance at Oil-
field Coulee are two species of Platanaceae (Figs.
56, 57). Both are large, rhombic leaves with pal-
inactinodromous venation, pectinal veins, nip-
ple-shaped teeth, and orthogonal tertiary and
quaternary venation.

Much of the diverse Oilfield Coulee flora can-
not be treated fully here. One leaf species (Dicot
17, not figured) is entirely consistent with the
leaf morphology of extant Menispermaceae. Sev-
eral taxa of magnoliid-grade leaf morphology are
present (e.g., Fig. 55).

Other poorly known collections from the Two
Medicine exist (Appendix I). Because the Two
Medicine Formation extends upsection to the
top of the Campanian, and I have not revisited
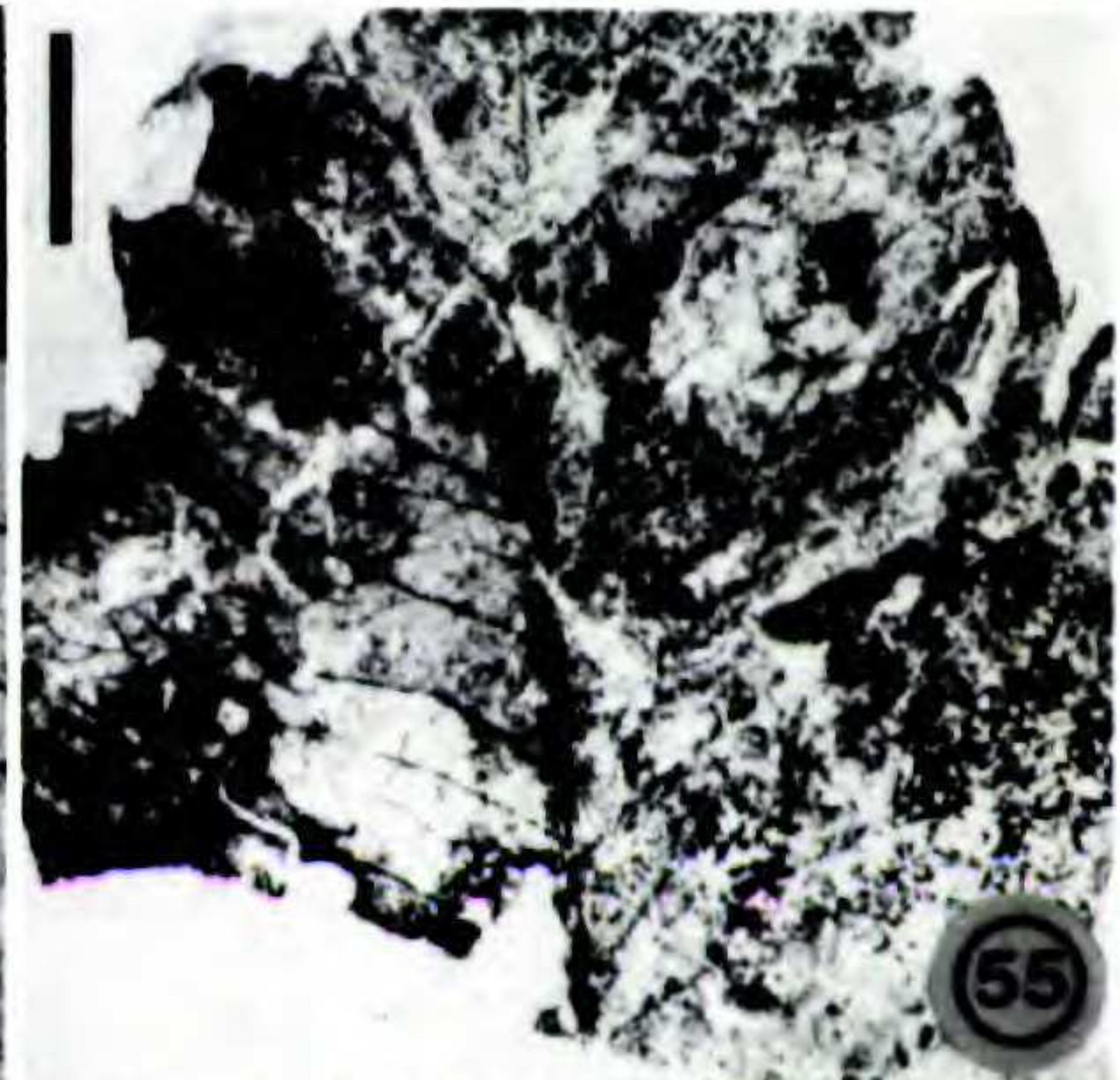
the collecting localities, it is difficult to assess the age of these collections. One specimen is illustrated (Fig. 47) from these localities. The leaf fits the Cinnamomophyll morphotype and may represent Laurales based on the presence of basilaminar secondary veins, basal secondaries at a lower angle than superadjacent secondaries, admedial orientation of tertiary venation, subparallel and irregularly branched quaternary venation, and possible mesophyll secretory bodies.

MIDDLE CAMPANIAN FLORAS

Floras are known from the Judith River Formation in central Montana (Knowlton, 1905) and the Oldman Formation in southern Alberta (Penhallow, 1908; Bell, 1963, 1965). The two floras were recovered from fluvial sandstones and exhibit a similar composition. Simple leaves with serrate margins and pinnate, craspedodromous venation allied to Hamamelidaceae predominate. There is some evidence for the presence of Trochodendrophylls (Hickey, 1984). Diverse Platanophylls, including "Platanus" affinis Lesquereux, are found in the Oldman flora. "Artocarpus" sp. (Bell, 1965) from the Oldman is a pinnately compound leaf, the leaflets of which are pinnately veined with eucamptodromous secondary veins and many intersecondaries. This morphology relates it to rosid groups, including Sapindales, Rutales, and Rosales. Dawson (1886, 1887) described plants from the Belly River series, which is equivalent to the Judith River–Oldman floras. His species appear unusually advanced for the Campanian, an attribute Knowlton (1900) ascribed to stratigraphic mixing of the collections. Ramanujan (1972) reported on permineralized coniferous woods of Taxodiaceae and Podocarpaceae from the Oldman Formation.

Several other lower and middle Campanian floras exist from the NRM region. They are the Allison flora from southwest Alberta (Berry, 1929d), the Maudlow flora (Skip & McGrew, 1977), and the Livingston flora (Knowlton, 1893) from southcentral Montana, the Adaville flora from southwest Wyoming (Dorf, 1955), and the Point of Rocks flora from southcentral Wyoming (Brown, 1956; Dorf, 1955; Knowlton, 1900; Lesquereux, 1878; Newberry, 1898; Ward, 1885, 1887).

SUMMARY

During an approximate three million year period of the Middle and Late Albian, angiosperms displaced gymnosperms as the dominant lowland vegetation of the NRM region. This occurred shortly after the entry of angiosperms into the region. Upland vegetation retained a predominantly gymnospermous composition. Pteridophytes remained important through this period, although composition changed. Ginkgophytes, Cycadophytes, and Pteridosperms decreased dramatically.

Although the arrival of angiosperms can be seen as the essential agent of change, several environmental factors correlate with the floristic changes in the Albian. The Cretaceous epeiric seaway expanded across the mid-continent for the first time during the Albian. Climatic seasonality may have increased due to increased orogenic activity in the Cordillera and increased temperatures.

Early angiosperms with low rank leaves such as Rogersia and Ficophyllum are not recognized in the NRM region. The Middle Albian flora is closely allied to time equivalent floras at lower latitudes in North America. The similarity is most pronounced at the level of genus, although a few species appear to have ranged across North America during this time. As in the Potomac flora, Sapindophylls and Platanophylls form a conspicuous element. Other groups, such as the Cinnamomophylls and Pentalobaphylls, appear to have achieved prominence earlier in the NRM region than elsewhere in North America and impart a uniqueness to the regional flora.

Leaf morphologies indicate that early mem-

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FIGURES 48–58.   Angiosperm megafossils from the Two Medicine Formation. Specimen numbers correspond to the research collection housed at the Department of Botany, University of Montana. 48–57. "Oilfield Coulee" locality.—48. Pinnate palm, 23A/M1/003.—49. Rutales?, Dicot 43, 56A/43/001.—50. Dilleniidae, Dicot 1, 40A/01/001.—51. Trochodendrales, Dicot 11, 50A/11/001.—52. Cercidiphyllales, Dicot 53, 57A/53/001.—53. Indeterminate leaf with craspedodrome secondaries, strong basal secondary veins, and chloranthoid teeth, Dicot 50, 55A/50/001.—54. Hamamelidaceae, Dicot 25, S174A/25/010.—55. Magnoliid-grade leaf of uncertain affinity, Dicot 27, 39B/27/002. 56, 57. Platanaceae.—56. Dicot 32, HPC/32/022.—57. Dicot 6, 24A/06/021.—58. Laurales, USGS locality 6015.
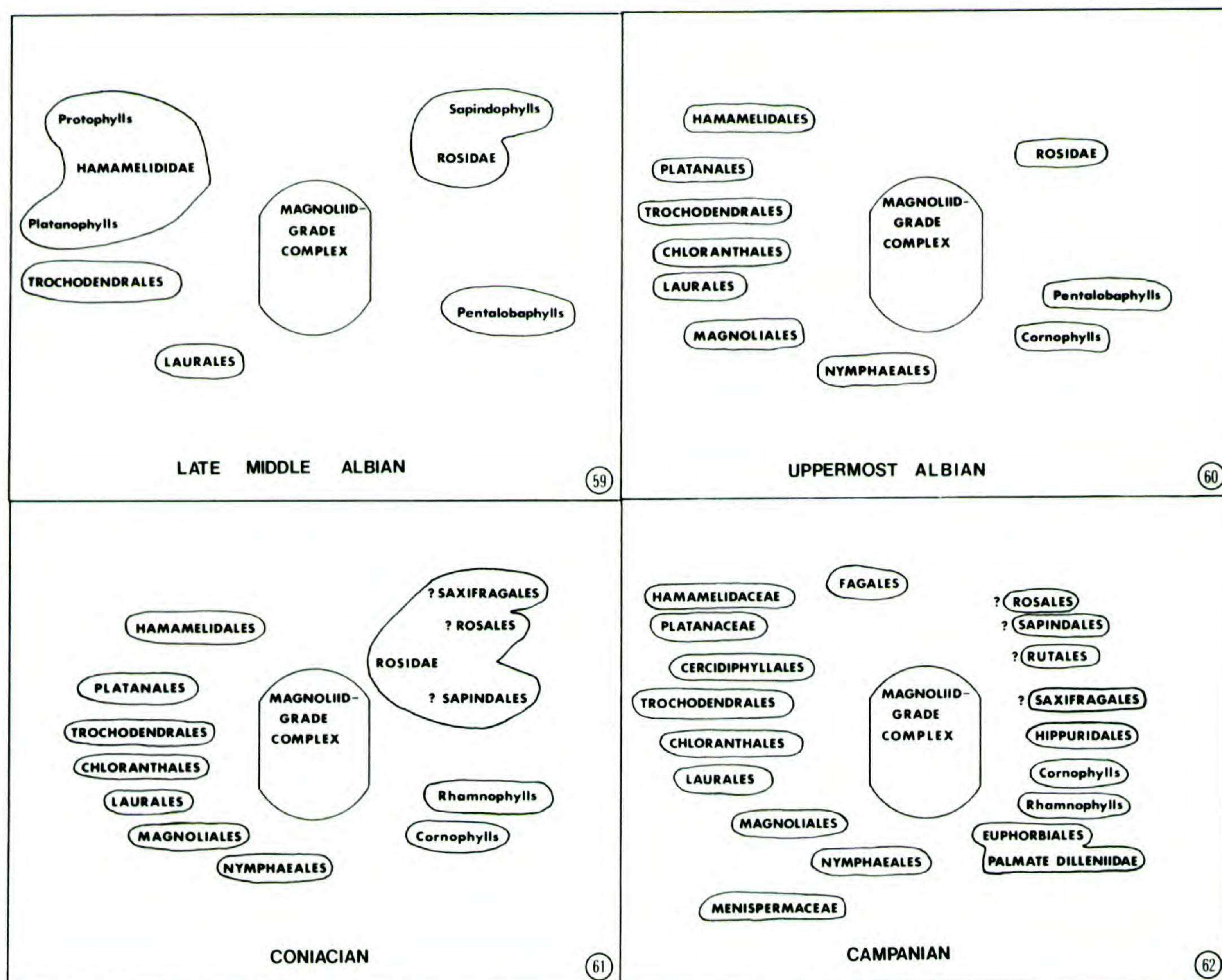
FIGURES 59–62.   Changing diversity and floristic affinity of the pre-Maastrichtian dicotyledonous flora of the northern Rocky Mountain region. Occurrences of taxa are based on interpretation of leaf morphology except in the following cases: Chloranthales (*Clavatipollenites*), Hippuridales (*Retitricolpites microreticulatus* Brenner), Fagales (*Tricolporopollenites* sp.), and Euphorbiales (*Erdtmanipollis*). Muller (1981) accepted these occurrences as indicative of the presence of the taxa (see also Norris et al., 1975; Rouse et al., 1971).

bers of several Recent higher taxonomic categories of angiosperms existed in the Albian flora (Figs. 59, 60). Sapindophylls appear to be allied to primitive Rosidae. Hamamelididae is well represented by Platanophylls, Protophylls, and Trochodendrophylls. Magnoliidae allied to Laurales, Magnoliales, Chloranthales, and Nymphaeales are probable. Monocotyledons are not apparent in the megaflora of the NRM region until the Late Cretaceous.

The early angiosperm flora includes several prominent groups with no clear relationship to Recent taxa (Table 1). Pentalobaphylls exhibit some affinity with Rosidae and Magnoliidae. The morphotypes Cinnamomophyll, Rhamnophyll, Cornophyll, and Magnoliaephyll are informal categories based on leaf morphology. The names do not imply relationship to any modern group, merely convergence in leaf morphology with

modern forms. Much of the diversity of early dicotyledons is manifest in these morphotypes. New higher level taxa will probably be necessary to allow for their adequate classification.

Cenomanian floras in the region retain some older elements (Platanophylls, Protophylls, Cinnamomophylls, and Trochodendrophylls are worthy of mention), but on the whole are more modern in aspect, contain higher rank leaves, and are more diverse than Albian floras. Latest Albian and Cenomanian floras from lower latitudes within the region contain Dryophylls and *Dewalquea*.

Post-Cenomanian floras continue to diversify, attaining levels of advancement consistent with several modern orders and families (Figs. 61, 62). Hamamelididae (Platanaceae, Trochodendrales, Hamamelidaceae, Cercidiphyllales, and Fagales), palmate Dilleniidae, and Rosidae are a

persistent part of the flora. Magnoliidae (Laurales, Chloranthales, Nymphaeales, and Magnoliales) appear as members of individual floras. Ranunculiidae (Menispermaceae) is recognized from the lower Campanian in Montana. Pinnate palms date from the Lower Campanian. The group is historically associated with stream margin environments.

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APPENDIX I

LOCALITY INFORMATION, CHRONOSTRATIGRAPHIC REFERENCES, AND LOCATIONS OF COLLECTIONS FOR NORTHERN ROCKY MOUNTAIN REGION FLORAS

Megafossil collections referred to in this report are listed below in alphabetical order. Numbers in parentheses following name of collection correspond to those used in Figures 2 and 3 and in Tables 2 and 3. Chronostratigraphic references are placed in parentheses immediately following the age. Specific locality information is provided only for collections that have not been published or have been published but with locality information absent or sketchy. All others are referenced to the publications that provide locality specifications. Institutions where collections are housed are indicated.

ALBINO (1). Upper Upper Albian (Roberts, 1972). I made a small collection from leaf mats in the Albino Member of the Mowry Formation along Beaver Creek, Gallatin County, Montana. This locality is in pink and white volcaniclastic siltstones of the Albino Member of the Mowry Formation in the NW ¼, SW ¼, sec. 18, T. 7 S, R. 4 E. Collections are housed at the Department of Botany, University of Montana. An extensive fern flora is also known from the Albino Member (Crabtree, 1983).

ASPEN (2). Upper Upper Albian (Cobban & Reeside, 1952a; Nichols & Jacobson, 1982). This collection is from the predominantly marine Aspen Formation at USGS locality 8168 located in the NW ¼, sec. 6, T. 24 N, R. 115 W northwest of Kemmerer, Lincoln County, Wyoming. The formation is 1,000 feet thick here, and the plants occur 125 feet from the top (Brown, 1933a). Collections are housed at the U.S. National Museum.

BADHEART (3). Lower Santonian (Stott, 1961, 1963; Bell, 1963). Collections are from the Badheart Formation in the vicinity of Belcourt Ridge, eastcentral British Columbia. Collections are housed at the Geological Survey of Canada.

BEAVER MINES (4). Lower Middle Albian (Bell, 1956; Mellon, 1967; Mellon & Wall, 1963; Stott, 1968; Singh, 1971). Collections are from the Beaver Mines Formation in the vicinity of Crowsnest Pass, southwest Alberta. Collections are housed at the Geological Survey of Canada.

BLACKLEAF (5, 19, 20). Lower Upper Albian (Cannon, 1966; Rice & Cobban, 1977). Collections come from several USGS localities in the Vaughn Member of the Blackleaf Formation in northwestern Montana. Col-

lections are described under three headings which correspond to geographic locations:

Black Eagle (5). The single locality is in the NW ¼, SE ¼, NE ¼, sec. 13, T. 21 N, R. 3 E about 5 km north of Great Falls, Cascade County, Montana. Collections are housed at the Department of Botany, University of Montana.

Summit (19). Collecting localities are scattered for about 10 km along the east side of Marias Pass along the Burlington Northern Railroad, USGS field localities 5984, 5985, 5986, 6007, and 9439 in Glacier County, Montana. A separate area exists on the west side of the pass in the S ½, sec. 1, T. 29 N, R. 14 W Flathead County, Montana. Collections are housed at the U.S. National Museum with the exception of a small collection from ½ mile west of Marias Pass, which is at the Department of Botany, University of Montana.

Sun River (20). USGS locality 9437 from the SW ¼, SE ¼, NE ¼, sec. 36, T. 22 N, R. 13 W on the north side of the Sun River, Teton County, Montana. Collections are housed at the U.S. National Museum.

COMMOTION (6a, 6b, 6c). Collections are from three members of the Commotion Formation and are housed at the Redpath Museum and the Geological Survey of Canada. Each member is treated separately below.

Lower Gates (6a). Lower Middle Albian (Bell, 1956; Mellon et al., 1963; Stott, 1960, 1968; Singh, 1971). Collections are from the lower Gates Member in the vicinity of Pine River, northeast British Columbia.

Upper Gates (6b). Middle Middle Albian (Bell, 1956; Mellon et al., 1963; Stott, 1960, 1968; Singh, 1971). Collections are from the upper part of the Gates Member along Belcourt Ridge, eastcentral British Columbia.

Boulder Creek (6c). Middle Middle Albian (Bell, 1956; Stott, 1968; Singh, 1971). Collections are from the Boulder Creek Member in the vicinity of Pine River, northeast British Columbia.

CROWSNEST (7). Lower Upper Albian (Bell, 1956; Mellon & Wall, 1963; Mellon, 1967). Collections are from the Mill Creek Formation in the vicinity of Crowsnest Pass, and along the eastern side of the Front Range in southwest Alberta. Collections are housed at the Geological Survey of Canada.

DUNVEGAN (8). Cenomanian (Bell, 1963; Stott, 1960, 1968). Collections are from the Dunvegan Formation in the vicinity of Pine, Smokey and Peace rivers, northwest Alberta and northeast British Columbia and are housed at the Redpath Museum and the Geological Survey of Canada.

EAGLE (9). Lower Campanian (Cobban & Reeside, 1952a; Russell, 1970). The Eagle flora reported by Knowlton (1900) was collected by Lester Ward in 1883. Knowlton's description of the location is vague: "the south side of the Missouri River near Bear Creek." Knowlton's specimens, several of them types, are missing from the U.S. National Museum.

I attempted to relocate Ward's site and found a small assemblage from along the Missouri River below Rattlesnake Coulee about 12 km south of Coal Banks, Chouteau County, Montana, in section 24, T. 26 N, R. 12 E. This collection is at the Department of Botany, University of Montana.

Bell (1963) reported a flora from Buckley and Red

Coulees, Toole County, Montana, in the vicinity of the International Boundary south of the town of Milk River, Alberta (see Evans, 1930). I was unable to locate this collection at the Geological Survey of Canada.

In recent years, collecting has been carried out at USGS locality 7633 from the Eagle Formation by L. J. Hickey in Elk Basin, Park County, Wyoming, in the SE ¼, NE ¼, NW ¼, NW ¼, sec. 21, T. 58 N, R. 99 W. His collections are housed at the U.S. National Museum.

FALL RIVER (10). Upper Albian (Crabtree, pers. obs.). While at the U.S. National Museum I examined several specimens from USGS locality 7312 in the general collection. The ledger of field collection sites indicates that these plants were found in the Fall River Sandstone near Pine Creek, Wyoming. This is probably the Pine Creek mentioned by Ward (1899). As best I can judge from Ward's descriptions, the fossils are from R. 62 W, T. 55 N in Crook County, Wyoming, from a level 60 feet below the Dakota contact. This locality could be as old as Middle Albian.

FRONTIER (11a, 11b). Two main stratigraphic levels in the Frontier Formation have yielded plant megafossils. These are treated separately below.

Lower Frontier (11a). Lower Cenomanian (Cobban & Reeside, 1952b; Nichols & Jacobson, 1982). Many collections were made from the lower Frontier Formation as the result of geological fieldwork. Hall (1845) reported on the earliest collections from the Frontier made by the Charles Fremont Expedition. This site was apparently along Little Muddy Creek, Lincoln County, Wyoming, in the S ½, sec. 29, T. 19 N, R. 116 W. U.S. Geological Survey collections from this area and the adjacent sec. 6, T. 18 N, R. 116 W include USGS field localities 8676, 3671, 5048, and 5049. Knowlton (1917) reported on collections primarily from locality 5049. Subsequent collections from this and nearby localities were reported by Andrews & Pearsall (1941). All of these localities are from the same stratigraphic level about 1,200 feet below the Oyster Ridge Sandstone and are considered to be of lower Cenomanian age. Hall's original collection no longer exists. Knowlton's published collections are housed at the U.S. National Museum. Andrews's collection, primarily ferns, is at the Department of Biological Sciences, University of Connecticut. Unstudied collections are at the U.S. National Museum.

Upper Frontier (11b). Turonian (Nichols & Jacobson, 1982). Collections from the Frontier near Lander, Wyoming (Berry, 1929d) are from well above the Oyster Ridge Sandstone. These collections are housed at the U.S. National Museum.

JACKASS MOUNTAIN (12). Middle Middle Albian (Bell, 1956). Collections are from localities in the Jackass Mountain Formation in southcentral British Columbia and are housed at the Geological Survey of Canada.

JUDITH RIVER-OLDMAN (13). Middle Campanian (Cobban & Reeside, 1952a; Russell, 1970). The collections from the Judith River Formation described by Knowlton (1905) were collected at USGS locality 3272 along Willow Creek about 1.4 km east of old Fort Maginnis, Musselshell County, Montana. I can find no locality information for the Oldman Formation in southern Alberta, but see Ramanujan (1972) and Bell

(1965). Judith River collections are housed at the U.S. National Museum.

KINGSVALE (14).   Middle Middle Albian (Bell, 1956). From localities in the Kingsvale Formation in south-central British Columbia. Collections are housed at the Geological Survey of Canada.

MILK RIVER (15).   Lower Campanian (Bell, 1963; Russell, 1970). Localities are in the Milk River Formation along Milk River, south Alberta (Bell, 1963). Collections are housed at the Geological Survey of Canada.

MILL CREEK (16).   Lower Upper Albian (Mellon & Wall, 1963; Mellon, 1967). Collections are from the Mill Creek Formation near Crowsnest Pass and north along the foothills in southeast Alberta. They are housed at the Geological Survey of Canada.

PASAYTEN (17).   Middle Upper Albian (Barksdale, 1975; Bell, 1956). From the Pasayten Formation in southcentral British Columbia. Collections are housed at the Geological Survey of Canada. The specimen in Figure 27 is at the Department of Botany, University of Montana.

PRE-MUDDY (18).   Middle Middle Albian (Roberts, 1972). S. Vuke made this collection from beds below the Muddy Sandstone along Buck Creek, Gallatin County, Montana, in T. 8 S, R. 3 E. It is housed at the Department of Botany, University of Montana.

TWO MEDICINE (21).   Lower Campanian (Russell, 1970; Lorenz, 1981). Collections are from the lower part of the Two Medicine Formation in "Oilfield Coulee" about 20 m above the contact with the Virgelle Sandstone in the SW ¼, sec. 18, T. 32 N, R. 5 W about 6 km south of Cut Bank, Glacier County, Montana. These are housed at the Department of Botany, University of Montana. Unstudied collections from USGS localities 6009, 6010, 6011, 6013, 6015, 6129, 6388, 6390, 8574, and 9449 in Glacier County, Montana, are housed at the U.S. National Museum.

WAYAN (22).   Upper Upper Albian or Lower Cenomanian (Cobban & Reeside, 1952a; Moritz, 1953). During the course of many years, an amateur collector named Thomas Henry made a very large collection of *Tempskya* and other fossils from the Wayan Formation in the vicinity of Wayan, Caribou County, Idaho. The exact locality (-ies) is not known, but appears to have been in sec. 24, T. 5 S, R. 43 E and secs. 19 and 20, T. 5 S, R. 44 E. I could not relocate the sites during my own visits to the area in 1983. Most of the Wayan material is housed at the Department of Geology, Idaho State University. The specimens figured in this report (Figs. 21–23) are housed in the Department of Botany, University of Montana.

WINTHROP (23).   Upper Albian or Cenomanian (Barksdale, 1975; R. Rau, pers. comm.). Collections housed at the U.S. National Museum and reputed to be from the Winthrop Formation are probably Paleocene in age (J. Wolfe, pers. comm.). Material in this report was collected by myself, R. Rau, and J. Robison from the type locality of the Winthrop Formation near the Boesel Ranch along the Methow River road in the NW ¼, NE ¼, SE ¼, sec. 14, T. 35 N, R. 20 E, Okanogan County, Washington. This collection is housed at the Department of Botany, University of Montana.